

A REVISION OF STYRAX (STYRACACEAE) IN NORTH AMERICA, CENTRAL AMERICA, AND THE CARIBBEAN

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The *Styracaceae* consists of about 12 genera, all small except *Styrax*, and about 150 species centering in eastern Asia, but with numerous species in the New World, none in Australia, one in the eastern Mediterranean region, and about three in Africa. The characters distinguishing *Styrax* from other genera in the family are: stamens 10 or more; flowers perfect, in racemes, cymes, or panicles; ovary completely or almost completely superior; seeds not winged; filaments free or connate only in the lower part; and fruit drupaceous. Two of the genera, *Alniphyllum* and *Pterostyrax* (China and Japan), are considered most closely related to *Styrax*. *Alniphyllum* differs from *Styrax* in its winged seeds, filaments connate to the top into a tube, and capsular fruit, while *Pterostyrax* differs in its two-thirds to completely inferior ovary (Hutchinson, 1959).

Styrax, a genus of trees and shrubs, is cosmopolitan in its distribution and includes about 120 species, most of which are tropical and subtropical. It occurs in eastern Asia, New Guinea, the eastern Mediterranean region, the Caribbean, South America, Central America, and North America. Ecologically, the species occupy habitats from high mountainous regions to swamps.

Economically and horticulturally the genus is of substantial value. Many species are planted as ornamentals either singly on lawns or in hedges and fencerows. The white-flowered, pendulous racemes and spreading habit make these plants a noteworthy addition to any landscape. In addition to the ornamental value, several species of the Mediterranean region are the source of the aromatic resins styrax and benzoin.

This study is a reappraisal of *Styrax* in North America, Central America, and the Caribbean. The taxonomic status of many of the previously described species is doubtful. Some authors seem to have exploited the genus in order to name new species. This trend is reflected in Standley and Steyermark's (1940) statement describing *Styrax vulcanicola*:

The most closely related species is the recently described *Styrax magnus* Lundell, of the Volcan de Tacana, Chiapas. In that the shape and size of the leaves suggest *Styrax vulcanicola*, but the pubescence consists of much larger, relatively lax, soft, spreading hairs, making it fairly certain that two distinct species, as species of *Styrax* are divided, are represented.

These workers appear to have considered it justifiable to use frivolous characters to describe new species because other workers had done so. This trend was set by Perkins (1907), who monographed the genus and caused much confusion by finely and unnecessarily dividing the species complexes. Most species of the United States and Northern Mexico are quite distinct and easily delimited. However, difficulties arise in the southern Mexico and Central American species, primarily the *Styrax argenteus* complex. One of my main objectives is to clarify these matters.

Although this revision is based primarily on morphology, attempts have been made to consider phylogenetic relationships. Approximately 3,500 specimens from 16 herbaria were examined. These were augmented by my personal collection of many specimens from southeastern United States and southwestern Texas.

Complete citations for all species are given, with the exception of *S. americana* var. *americana* and var. *pulverulenta* and *S. grandifolia*. No more than five localities per state are given for *S. americana* var. *americana* and *S. grandifolia*. One locality per county is given for *S. americana* var. *pulverulenta*. Specimens most widely distributed in herbaria were selected for citation. A mimeographed list of collections examined may be obtained from me upon request.

The following herbaria provided *Styrax* specimens—the abbreviations are those of Lanjouw and Stafleu (1959): DUKE, F, FSU, GA, GH, LAF, MO, NCU, NY, OKLA, PH, SMU, TEX, UC, US, and VDB.

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GENERIC HISTORY

“*Styrax*” is the ancient Greek name for a fragrant resin used as incense and as medicine and for the plant (*Styrax officinalis*) from which it was obtained.

Accounts of *Styrax* were first given by Linnaeus (1735) in *Systema Naturae*. The genus was again treated by Linnaeus in *Species Plantarum* (1753) and *Genera Plantarum* (1754). The type species is *Styrax officinalis*.

Cavanilles (1790) described the genus *Strigilia* from material of *Styrax*. The type species, *Strigilia racemosa*, was later transferred by de Candolle (1844) to *Styrax* as *S. racemosa*.

Ruiz and Pavon (1794) applied the name *Foveolaria ferruginea* to a Peruvian species that was later transferred to *Styrax* by Perkins (1907) under the name *S. foveolaria*.

The generic name *Cyrtia* was applied by Loureiro (1790) to an element of

Styrax that was later transferred to *Styrax* under the name *S. agrestis* (Lour.) G. Don (Don, 1838).

The genus *Tremanthes*, described by Persoon (1805), included on publication all species of *Foveolaria* Ruiz et Pavon as well as the type of *Strigilia* Cav.

Perkins (1907) included *Foveolaria ferrugineum*, *Tremanthes ferrugineum*, and *Strigilia racemosa* in synonymy under *Styrax foveolaria*. If these relationships are true, then the name *S. foveolaria* is incorrect. All four names represent the same taxon, so the name *S. racemosa* (Cav.) A. DC. has priority since the specific epithet *racemosa* is the earliest given to this taxon.

Rafinesque's (1817) *Florula Ludoviciana*, significant as the first localized record of plants in southern Louisiana, was based on Robin's *Voyages dans l'interiere de la Louisiana, de la Florida et dans les Isles de la Martinique*. Robin's *Flore* (a section of *Voyages*) contains descriptions of plants observed by him from Louisiana east to Pensacola, Florida. Many of the plants described are without adequate names. In trying to correct these errors, and in order to place such species into proper relationships, Rafinesque proposed new names for many of the species. Rafinesque made a number of mistakes since he had to work solely from written descriptions and illustrations and since he was not familiar with the flora of the region. In *Florula Ludoviciana* he named what he considered a new genus, *Adnaria*, and its only species, *A. odorata*. Robin had placed this shrub in the "Campanulacees" under *Campanula*, but Rafinesque recognized that it did not belong to that group and suggested that it was a member of the "Vaccinia." Camp (1941) visited the area where *Adnaria* was said to have grown and found and identified the plant as *Styrax americana*. Camp said that the mistake in identification was caused primarily by Robin because Rafinesque was probably not familiar with *S. americana* in the field, but Robin listed and described *S. americana* in his *Flore*.

The generic name *Epigenia* was proposed by Velloso (1825). Shortly thereafter, Schott (1827), transferred all species of *Epigenia* to *Styrax*.

Styrax benzoin was described by Dryander (1787). Hayne (1829) described a new genus, *Benzoin*, the type species being *B. officinalis*. Roxburg (1832), recognized Hayne's error and listed *B. officinalis* as a synonym of *Styrax benzoin*.

The most recent generic name associated with *Styrax* is *Darlingtonia*, published by Torrey in 1851. Torrey (1853) later stated, "and a California plant, on imperfect specimens of which, I had recently indicated a genus under this name, proves to be only a species of *Styrax*." Torrey's combination, *Darlingtonia californica*, was conserved in this publication and applied to a member of the *Sarraceniaceae*. The new styrax he named *S. californica*.

During the later part of the 19th and the early 20th century numerous works treated *Styrax* from areas of North America, Mexico, and the Caribbean. In addition to large treatments such as those by de Candolle (1844), Bentham and Hooker (1876), Gurke (1897), and Baillon (1892), which all

treated the *Styracaceae*, the most comprehensive and recent work is the monograph of *Styrax* by Perkins (1907). Perkins confused the taxonomy of the group by describing numerous new species many of which have proved not to be "good" taxa.

MORPHOLOGY

Life Cycle. The following general life cycle was formulated during my study from observations made on *Styrax grandifolia* and *S. americana* (southeastern United States).

The winter buds unfold from late February through early March. The internodes elongate and the leaves expand and reach full size in late March or April. At the same time, the inflorescence develops. Before the winter buds unfold, the synsepalous calyx and the separate corolla lobes and stamens develop more or less simultaneously.

As the leaves reach full size, the corolla begins to project from the calyx. The aestivation of the corolla lobes may be imbricate or valvate depending on the subgenus. The gynoecium has developed by this time, and the lumen is expanded by a mass of tissue that later becomes the placentae.

The flowers generally open about mid-April to mid-May. The period of flowering is normally 2-3 weeks for temperate species and somewhat longer for tropical and subtropical species. The flowers have a faint sweet odor and attract a variety of insects of which various bees seem the most active pollinators. Although the stamens have introrse dehiscence, they are reflexed considerably, this causing any visitor to be dusted with pollen. The flowers of most species remain open 3-5 days, after which the corolla lobes lose their turgidity and corolla and stamens are shed. Within a week after the fall of the corollas many ovaries are visibly swollen.

Dissection of an ovary during the early stages of swelling reveals usually one but sometimes two developing ovules. The ovary or young fruit soon expands so as to rupture the calyx and extend beyond it. The fruit ripens from July through September and eventually opens by one or more sutures. The seed coat is primarily a mass of stone cells forming a hard and brittle shell. The cotyledons are large and elliptic. There is a massive hypocotyl, but the plumule is scarcely detectable. The seeds often germinate in close proximity to the parent plant, resulting in dense stands.

Habit. The storaxes are shrubs to medium-sized trees with a rather loose, spreading habit. The numerous, white, fragrant flowers, borne either singly or more often in few-flowered racemes, are followed by drupaceous fruits.

Species of *Styrax* native in the United States are generally large shrubs, occasionally reaching tree size. *Styrax grandifolia* of the eastern United States often has a rather flabellate branching system and a rounded crown. The southwestern Texas and California species are medium-sized shrubs, rough in outline due to a somewhat irregular branching pattern. South through Mexico the species are progressively larger. *Styrax argenteus* of southern Mexico and Central America reaches a height of 30-35 ft., having

a rather freely branched crown and spreading habit. One of the largest species, *S. glaber*, which occurs in the Caribbean, reaches a height of 40 ft. but still has a somewhat spreading habit.

The storaxes are generally understory shrubs or trees in the eastern United States but are often exposed shrubs in the southwestern and western United States. Those reaching tree size in Mexico and Central America often form a substantial part of the forest canopy or forest edge.

Stem. The stems have smooth tight bark to rough flaky bark and may be glabrous to densely pubescent. Cork forms in the inner cortex, which includes a closed or slightly interrupted ring of sclerenchyma. Secondary phloem includes sclerenchymatous elements. The xylem forms a continuous cylinder traversed by narrow rays usually two to four (six) cells in width, markedly heterogenous. In the primary wood the vessels are narrow and scattered, with highly oblique, scalariform perforation plates. The fibers have bordered pits and are of medium length to moderately long. Parenchyma is diffuse and in regular uniseriate lines. The pith is solid. There are intercellular secretory cavities, containing balsamic resins, in the phloem, rays, and wood. Also, crystals of calcium oxalate are present in unlignified tissues (Metcalfe and Chalk, 1950).

Each leaf is supplied by a single vascular bundle, which is accompanied by a single gap in the stele (Sinnott, 1914).

Pubescence. Pubescence in *Styrax* is generally in the form of stellate trichomes, these differing widely in size and structure. The arms of the trichomes vary from especially long and straight as in *S. grandifolia* (Fig. 4d) and *S. argenteus* var. *hintonii* (Fig. 11b), to very short and stout as in *S. americana* var. *pulverulenta* (Fig. 3d) and *S. argenteus* var. *ramirezii* (Fig. 11c).

Four species possess lepidote trichomes: *S. portoricensis* (Fig. 15d), *S. glaber* (Fig. 16d), *S. ochraceous* (Fig. 14d), and *S. conterminus* (Fig. 12d). This type of trichome, very distinctive, is found predominantly on the lower leaf surface in these species. In *S. obtusifolia* of Cuba the lower leaf surface is covered with a light, fine tomentum mixed with scattered lepidote trichomes (Fig. 13d).

Some relationship can be seen in the trichomes of *S. platanifolia* var. *stellata* (Fig. 5f), *S. texana* (Fig. 6g), and *S. youngae* (Fig. 6h). The leaf shape and trichomes of the last two species very closely resemble those of *S. officinalis* var. *fulvescens* (Fig. 7f, 7g). However, *S. officinalis* var. *fulvescens* often has dimorphic pubescence—pale dense tomentum on the lower leaf surface and large dark brown or reddish-colored trichomes on the veins. These species, of rather arid regions, resemble one another in overall appearance.

Styrax jaliscana of northern Mexico might be related to the above-mentioned species. Although its leaves are more elliptic than suborbicular, the leaf texture and general appearance of the plant are very similar to *S. officinalis* var. *fulvescens*. However, its pubescence is woolly, the trichomes (Fig. 8d) having long slender arms very much like those of *S. grandifolia*.

The leaves of *S. youngae* and *S. jaliscana* have uniseriate hairs on the upper surface. These hairs are fairly long and are angled toward the apices of the leaves.

Styrax glabrescens var. *pilosus* bears a striking resemblance to *S. grandifolia* in overall morphology. The pubescence is much heavier on the leaves of the latter species, often becoming woolly, but both species have the same type trichomes with long slender arms (Figs. 9d, 4d).

In the *S. argenteus* complex there is variation in degree of pubescence: var. *ramirezii* (Fig. 11c) has stout trichomes with short arms; var. *hintonii* (Fig. 11b) has trichomes with long slender arms that very much resemble those of *S. grandifolia*; while var. *argenteus* (Fig. 11a) has trichomes of intermediate length.

The degree of pubescence on leaves and on flowering and fruiting structures is used as a major taxonomic character in several species complexes. These include *S. americana* and its variety *pulverulenta*, *S. platanifolia* and its variety *stellata*, *S. argenteus* and its varieties *ramirezii* and *hintonii*, and *S. glabrescens* and its variety *pilosus*.

Leaves. The leaves vary much in size, shape, and texture, ranging from broadly obovate to elliptic-oblong or semi-orbicular and from thin and fine to thick, coriaceous, and revolute. Many of these differences are employed taxonomically in this treatment. Leaf shape and geographic range together are good characters for separating several groups of species. *Styrax grandifolia*, occurring in the eastern United States with *S. americana* var. *pulverulenta*—whose leaves may be also densely pubescent below—can be distinguished from the latter species by its rather large, obovate leaves in marked contrast to the smaller elliptic leaves of var. *pulverulenta*. The suborbicular leaves of *S. platanifolia*, a species of southwestern Texas and northern Mexico, are distantly toothed toward the apices and cannot be confused with any other species in this study.

Stomata are confined to the lower leaf surface. The vascular bundles of the smaller veins are accompanied by sclerenchyma. A transverse section through the distal end of the petiole reveals a median, cylindrical, vascular strand flattened towards the adaxial surface. Solitary and clustered crystals, probably of calcium oxalate, are reported to occur, especially around the vascular bundles (Metcalfe and Chalk, 1950).

The epidermal pattern of the leaves of *Styrax* is of both the regular- and the irregular-celled type. Although it is not likely that epidermal-cell form could be used as a specific taxonomic character, it is possible to see affinities between species said to be closely related. A study of epidermal cells reveals some possible relationships between the species of *Styrax*.

In addition to the stellate pubescence, occasional scattered glands occur on the lower leaf surface. These glands, rather flattened and circular, are composed of from five to eight small cells surrounding a central depressed area; the function is unknown.

A leaf-clearing technique, including the tannic acid-ferric chloride stain-

ing procedure of Foster (1934), was used for studies on the epidermal cells.

Flowers. The inflorescences are terminal or axillary, and have numerous white- or cream-colored, fragrant, often pendulous, solitary or racemose flowers. The pedicel of each flower is subtended basally by minute leaflike bracts. These bracts often also occur midway on the pedicel and on the calyx. The length of the bracts varies with the species.

The calices of *Styrax* are campanulate, with the lobes reduced to teeth. The teeth vary from five to seven and range from inconspicuous as in *S. argenteus* to long acute-acuminate as in *S. jaliscana*. The calyx surfaces vary from glabrous and smooth, as in *S. americana* var. *americana*, to densely stellate pubescent, as in *S. argenteus* var. *hintonii*. The size of the teeth and the presence or absence and degree of pubescence may be used as taxonomic characters. The calices are persistent on the drupaceous fruits.

The corolla is sympetalous, the tube being from 3–5 mm long. For this distance the stamens are completely adnate to the tube. The white- or cream-colored lobes number usually five, occasionally six. They are linear-oblong to elliptic-oblong or obovate and range, depending on the species, from 5 mm to 2.8 cm long. The lobes may remain straight, partially open, or widely flared, or the apices may be strongly reflexed. An unusual condition exists in *S. ochraceus* in that the lobes, up to 2.8 cm long and sympetalous basally, are partially fused for two-thirds their length with the apices reflexed. The effect is that of a long salverform corolla.

Perkins (1907) divided *Styrax* into two sections, *Eustyrax* and *Foveolaria*. *Eustyrax* includes those species having 16–24 ovules per ovary while *Foveolaria* includes those having 3–5 ovules per ovary. *Eustyrax* was divided into two series, *Valvatae* and *Imbricatae*. *Valvatae* represents those species having valvate dehiscence of the corolla lobes; *imbricatae*, those with imbricate dehiscence. The species in *Valvatae* has lobes that are rather thick, often with a reddish tint on the inner surface. These include *S. argenteus* and its varieties, *S. conterminus*, *S. portoricensis*, *S. obtusifolia*, and *S. glaber*. The other species included in this study are in *Imbricatae*; their corolla lobes are rather thin and have the same color and texture on both surfaces.

A nectary was not detected at the base of the corolla; however, the flowers are often aromatic and attract a variety of insects. Copeland (1938) reports, of *S. officinalis* var. *californica*, that minute drops of liquid have been seen on the distal part of the ovary, but no taste of nectar was detected.

The stamens are usually twice as many as the corolla lobes, monadelphous in a short tube basally, 4–6 mm long, and adnate to the sympetalous corolla tube but extending just beyond it. *Styrax ochraceus*, which characteristic-ally has long corolla lobes, has filaments fused nearly the entire length of the partially-fused corolla lobes.

The anthers are basifix, with linear introrse dehiscence. The filaments are flattened and often stellate pubescent. The pollen, yellow and tricolpate, varies little in size, shape, and texture among the species.

The filiform style, exserted 1–3 mm past the stamens and about as long

as the corolla lobes, is usually glabrous but may be partially stellate-pubescent. The stigma is inconspicuously 3-lobed.

Fruit. The drupes, globose to oblong to broadly elliptic, are dry, loculicidally 3-valvate, and irregularly dehiscent or indehiscent. The one or rarely two seeds are subglobose to ellipsoidal with a basilateral hilum and a hard, smooth, or wrinkled testa. The cotyledons are large and elliptic, the hypocotyl is massive and the radicle and plumule are small.

The calyx is persistent. In several species the style, or part of it, remains on the fruit as an apiculation. Fruit characteristics are not generally used as taxonomic criteria in *Styrax*. *Styrax portoricensis*, however, has fruits so large that it cannot be confused with any other species in this study.

POLLINATING AGENTS

The flowers of *Styrax* are considered to be entomophilous. The anther sacs have longitudinal, introrse dehiscence, which is usually associated with self-pollination. However, the anther sacs are strongly reflexed, so that any visitor becomes dusted with pollen. Also, the style is longer than the stamens, which suggests an outbreeding system. Some wind pollination may also occur.

The pendant flowers are fragrant, and the rather wide, partially reflexed petals provide adequate landing sites for insects. Pollinators were observed on *S. americana* and on *S. grandifolia*. The following insects were most prevalent visitors:

Hymenoptera

- Apis mellifera*—Honey bee
- Bombus* spp.—Bumble bees
- Anthophora* spp.—Solitary bees
- Prosopis* spp.

Lepidoptera

- Danaus plexippus*—Monarch butterfly
- Eurema nicippi*—“Sleepy orange”

Diptera

- Fam. Blepharoceridae—The net-winged midges
- Fam. Drosophilidae
- Drosophila* spp.—Fruit flies

Thysanoptera

- Thrips tritiae*—Thrips

Of the Hymenoptera, *Apis mellifera* is the most frequent visitor, with several species of bumble bee next. The bumble bees have a more difficult time landing on the flowers than do smaller insects because the lax racemes do little to support their weight. Although the flowering period of *S. americana* and *S. grandifolia* lasts 2–3 weeks, insect visits are mostly during the first week. Those pollinators listed above were common on both species; however, more *Drosophila* frequented *S. americana*.

CYTOLOGY

Chromosome counts for several species of *Styrax* are found in the literature. Counts for *S. obassia* and *S. japonica* of Japan were made by Mansard (1936). In addition, chromosome counts for *S. officinalis* var. *californica* were made by Copeland (1938), and for *S. officinalis* var. *fulvescens* by Raven *et al* (1965). These counts are listed in Table 1.

During my study I attempted to obtain chromosome counts for *Styrax* of eastern United States, including *S. grandifolia*, and *S. americana* var. *americana* and var. *pulverulenta*. The counts were based solely upon pollen mother cell smears of freshly gathered material and are listed in Table 1.

The base number for *Styrax* is $n=8$. *Styrax grandifolia* was found to have a haploid number of 16 (Fig. 1c) and is, therefore, a tetraploid. Both *S. americana* var. *americana* and var. *pulverulenta* were found to have a haploid number of 8 (Fig. 1a, 1b), making them diploids.

The relationship between the eastern species of *Styrax* is confusing. It seems that the morphological distinctness of the taxa is maintained by internal rather than external isolating factors. Although the geographical ranges are sympatric, the ecological ranges rarely overlap. *Styrax grandifolia* is more prevalent on rather dry, well-drained, sandy soils, commonly on slopes. It covers a wide range, most of which it shares with *S. americana*. Where the ecological ranges overlap there is no indication of hybridization between the species.

There are at least two possible origins of *S. grandifolia*. Wood and Channell (1960) noted that *S. glabrescens*, whose range includes northern Mexico, is a close relative of *S. grandifolia*. No chromosome counts are available for *S. glabrescens*, but the two species show very close morphological resemblance. *Styrax grandifolia* also resembles *S. officinalis* and has been misidentified as this species—as in Walter (1788). The resemblance to *S. officinalis* is indeed striking on some specimens collected on high, well-drained, sandy soils. *Styrax officinalis* (a known diploid) is principally a Mediterranean species whose range also includes California. It may have ranged further east in North America in ages past. *Styrax grandifolia* could have arisen as an allo- or autotetraploid from the above species or possibly from *S. americana*. Further work on the genomic characteristics is necessary to make any definitive statements.

The origin of *S. americana* is even more perplexing. Other than *S. japonica*, there are no other species that, on morphological grounds, would have given rise to *S. americana*. *Styrax japonica*, a pentaploid whose range does not include North America, seems a most unlikely ancestor.

A great deal more cytological work needs to be done in order to assemble conclusive evidence of the evolutionary relationships of the species of *Styrax*.

As with many woody plants, it was rather difficult to determine the chromosome number, and it was only after many attempts that the counts for *S. grandifolia* and *S. americana* were obtained. There seems to be a very narrow time range within which meiosis occurs in *Styrax*.

TABLE I. Chromosome Counts ($2n$) for *Styrax*.

Species	$2n$ Number	Source of Count
<i>Styrax obassia</i>	16	Manshard (1936)
<i>Styrax officinalis</i> var. <i>californica</i>	16	Copeland (1938)
<i>Styrax officinalis</i> var. <i>fulvescens</i>	16	Raven <i>et al.</i> (1965)
<i>Styrax americana</i> var. <i>americana</i>	16	Gonsoulin (Louisiana: Washington Parish. Bogalusa. <i>Gonsoulin</i> 1032, 28 May 1969; flower buds collected 7 Mar 1970, 15 Mar 1972. NY, PH, SMU, US, VDB).
<i>Styrax americana</i> var. <i>pulverulenta</i>	16	Gonsoulin (Alabama: Baldwin Co. Foley. <i>Gonsoulin</i> 1964, 20 Mar 1973. Herbarium of East Tennessee State University).
<i>Styrax grandifolia</i>	32	Gonsoulin (Tennessee: Lewis Co. Gordonburg. <i>Gonsoulin</i> 1022, 3 May 1969; flower buds collected 6 Apr 1969. NY, PH, SMU, US, VDB).
<i>Styrax japonica</i>	40	Manshard (1936)

SYSTEMATIC TREATMENT

Styrax Linnaeus, Syst. Nat. ed. I. 1735; Gen. Pl. ed. I. 143. 1737; Sp. Pl. 444. 1753; Gen. Pl. ed. 5. 203. 1754.

Cyrtia Lour., Fl. Cochinch. 278. 1790.

Foveolaria Ruiz and Pavon, Fl. Peruv. Chil. Prodr. 57, t.9. 1794.

Strigilia Cav., Monadelph. Class. Diss. 7:358, t. 201. 1790.

Tremanthus Pers., Syn. Pl. 1:467. 1805.

Adnaria Raf., Fl. Ludovic. 56. 1817.

Epigenia Vell., Fl. Flum. 183. 1825.

Benzoin Hayne, Getr. Darst. Beschr. Arzneyk. Gew. 11, t. 24. 1829.

Darlingtonia Torr., Proc. Amer. Acad. Arts 4:191. 1851.

Shrubs or small trees of warm or temperate areas of the Americas and Eurasia. Leaves alternate, estipulate, commonly deciduous, entire or serrate-serrulate, broadly ovate-obovate to elliptic-lanceolate, densely stellate-pubescent to glabrous; apices mostly acute-acuminate; bases cuneate to rounded. Flowers perfect, 5-merous, in pendulous racemes in the axils of the leaves and/or on terminal branches; pedicels glabrous to densely stellate pubescent; calices campanulate, truncate, gamopetalous, 5-7-denticulate, glabrous to canescent or densely stellate-pubescent, fused basally, imbricate or valvate in the bud, eventually spreading or recurved. Stamens usually twice as many as the corolla lobes; filaments flattened, basally monadelphous, inserted near the base of the corolla; anthers oblong, basifix, with linear dehiscence. Ovary about half inferior to superior, 3-locular toward the

base, 1-locular above, ovules few to many in each locule; style simple, as long as or longer than stamens; stigma capitate, smooth or slightly lobed. Fruit globose to ovoid-oblong, dry, crustaceous, usually 1-seeded, irregularly dehiscent to indehiscent, basally surrounded by the persistent calyx. Seeds 1 or rarely 2, subglobose or elliptical with a basilateral hilum; testa hard, smooth or faintly wrinkled.

Type species: *Styrax officinalis* L.; common name: "Snow-bells."

There are about 120 species in the genus, most of them tropical and subtropical, in eastern Asia to New Guinea. (absent from the Philippines and Ceylon), the eastern Mediterranean region, South America, the West Indies, and Central and North America. Ten taxa occur in the United States, four of them varieties.

Parts of the following key were modified from keys of previous workers. These include the Series *Valvatae* and *Imbricatae* recognized by Gurke (1897) and Perkins (1907).

Key to North American,
Central American, and Caribbean
Styrax

1a. Corolla lobes predominantly valvate in aestivation. Series 1. *Valvatae*
1b. Corolla lobes predominantly imbricate in aestivation. Series 2. *Imbricatae*

Series 1. *Valvatae* Gurke

1a. Lower surfaces of the leaves covered either with long spreading stellate trichomes, or dense, matted or otherwise tomentose pubescence. 2
1b. Lower surfaces of the leaves glabrous or covered with scattered to dense lepidote pubescence. 3
2a. Leaves 7–14 cm long, oblong-elliptic, covered below with dense matted pubescence to dense long spreading stellate trichomes, apices short acuminate; mature flowers 13–17 mm long; central Mexico through Central America (Figs. 10 & 11). 9. *Styrax argenteus*
2b. Leaves 3–4 cm long, oblong to obovate, covered below with dense matted pubescence, apices rounded to acute; mature flowers 7–9 mm long; Cuba and Haiti (Fig. 13). 11. *Styrax obtusifolia*
3a. Leaves glabrous to covered with scattered lepidote pubescence below, the trichomes not commonly overlapping each other. 4
3b. Leaves completely covered below with lepidote pubescence imparting a crusty appearance. 5
4a. Leaf blades obovate-elliptic, 2–5 cm long, apices rounded to acute; mature flowers 2.5–3.4 cm long; drupes 8–10 mm long; Dominican Republic (Fig. 14). 12. *Styrax ochraceus*
4b. Leaf blades elliptic, 6–12 cm long, apices short acuminate; mature flowers 1.6–2 cm long; drupes 2.5–3.5 cm long; throughout Puerto Rico (Fig. 15). 13. *Styrax portoricensis*

5a. Mature flowers 12–15 mm long; drupes oblong-elliptic, slightly asymmetrical, 12–15 mm long; Central America (Fig. 12). 10. *Styrax conterminus*
 5b. Mature flowers 2–2.4 cm long; drupes ovoid to globose-ovoid, 2 cm long; throughout the British West Indies (Fig. 16). . . . 14. *Styrax glaber*

Series 2. *Imbricatae* Gurke

1a. Leaves orbicular to suborbicular or oblong-ovate; apices rounded to acute 2
 1b Leaves narrowly to broadly elliptic or obovate, apices acute to long acuminate. 7
 2a. Leaves glabrous or having sparse scattered coarse stellate pubescence. 3
 2b. Leaves with fine, dense, silvery indumentum to woolly white or grayish tomentum. 4
 3a Leaves irregularly lobed or toothed toward the apices; calices glabrous to finely puberulent, apices glandular and prominently toothed; Edwards Plateau, Texas, U.S.A. (Fig. 5). 3. *Styrax platanifolia*
 3b. Leaves not irregularly lobed or toothed toward the apices, lower surfaces glabrous to fulvescent; calices puberulent to fulvescent, apices non-glandular; Mediterranean region and California, U.S.A. (Fig. 7). 6. *Styrax officinalis*
 4a. Calices densely puberulent, their apices glandular tipped; leaves bright silvery below with a very fine and dense indumentum; Edwards Plateau, Texas, U.S.A. (Fig. 6). 4. *Styrax texana*
 4b. Calices and lower leaf surfaces not as above. 5
 5a. Lower leaf surfaces covered with dense woolly white tomentum, prominently veined; calices pale densely tomentose, the teeth very large, broadly acute; from Baja California through Central America (Fig. 8). 7. *Styrax jaliscana*
 5b. Lower leaf surfaces grayish tomentose to fulvescent; calices dark brown, the teeth wanting to moderately long and acuminate-attenuate. 6
 6a. Upper surfaces of the leaves covered with long spreading stellate trichomes, lower surfaces grayish tomentose; calices 4–5 mm long, 4–5 mm wide, teeth wanting to 0.4 mm long, style with stellate trichomes about 2/3 up from base; northern Mexico and the Davis Mts., Texas, U.S.A. (Fig. 6). 5. *Styrax youngae*
 6b. Upper surfaces of the leaves covered with short, close, stellate trichomes, lower surfaces having rufous, fulvescent pubescence, calices 5–7 mm long, 6–7 mm wide, teeth wanting to 1.2 mm long; style with stellate trichomes to 1/2 way up from base; Mediterranean region and California, U.S.A. (Fig. 7). 6. *Styrax officinalis*
 7a. Leaves generally broadly obovate, sometimes broadly ovate, apices acute to short acuminate, densely and finely tomentose below imparting a pale color; southeastern U.S.A. (Fig. 4). 2. *Styrax grandifolia*
 7b. Leaves narrowly to broadly elliptic, apices short to long acuminate, glab-

1. STYRAX AMERICANA Lamarck

Key to Varieties

Leaves oblong-elliptic, glabrous or sparsely trichomiferous on the undersurfaces and petioles, margins usually distantly toothed toward the apices; pedicels 10–14 mm long, calices 3–4 mm long, both essentially glabrous; new shoot growth and racemes glabrous to sparsely pubescent (Fig. 2).

1a. *S. americana* var. *americana*
Leaves elliptic to ovate, sparsely to densely scurfy-hairy on the undersur-
faces and petioles, margins entire to serrate; pedicels 4–6 mm long, calices
3–4 mm long, both densely scurfy-hairy; new shoot growth and racemes
rather densely matted pubescent (Fig. 3). 1b. *S. americana* var. *pulverulenta*

1a. *STYRAX AMERICANA* Lamarek var. *AMERICANA*, Encycl. Meth. Bot.

Styrax laeve Walt., Fl. Carol. 140, 1788.

Sturax glabrum Cav., *Monadelph. Class. Diss.* 6:340, t. 188. 1790.

Styrax laevigatum Ait., Hort. Kew. 2:75. 1789.

Styrax octandrum L'Her., Stirp. Nov. 2:t.

17 ex. Aiton, Hort. Kew. 2:75. 1789.

Halesia parviflora sensu Dendl., Bot. Reg. 11:t. 952. 1825, (non Michx. 1803).

Adnaria odorata Raf., Fl. Ludovic. 56. 1817.

Styrax americanus fma. *genuinus* Perkins, Pflanzenreich IV. 241
(Heft 30): 76. 1907.

Branded shrub, 1–4 m high. Leaves usually glabrous, blades oblong-elliptic, often ovate, 2–10 cm long, margin entire to serrate or distantly toothed, the bases cuneately narrowed, apices acute or short acuminate; upper surfaces dark green, glabrous; lower surfaces pale green, glabrous to faintly pubescent; petioles 3–5 mm long, glabrous to slightly pubescent. Flowers either solitary in the axils of the leaves or in axillary, semi-drooping, 2–7 flowered racemes; pedicels 10–14 mm long, glabrous to slightly pubescent; calices 3–4 mm long, pale, glabrous to slightly pubescent, teeth small, acute; corolla lobes 10–12 mm long, elliptic-oblong or lanceolate-oblong, lightly soft downy pubescent; stamens about as long as the corolla lobes; filaments short

pubescent on the proximal 1/3; anthers 1/3 the length of the stamens; style glabrous, about 1 mm longer than stamens; stigma barely if at all lobed. Drupes subglobose or obovoid, 6–7 mm in diameter, sparsely tomentose, style not persistent; seeds usually 1, globose, dark brown, dull (Fig. 2).

Found in rich soils, low, moist sites such as stream banks, floodplains, and margins of swamps. It ranges from northeastern West Virginia to southern Florida, westward along the Gulf Coast into eastern Texas, then north to southern Missouri, southern Illinois, southern Indiana, and Ohio (Fig. 17).

The usual flowering time for var. *americana* is from April through May; however specimens collected in Louisiana had flowers and fruit on the same branch as late as September. The colloquial name is “American snow-bell.”

Holotype: U.S.A. CAROLINAS AND GEORGIA. Michaux. Herbarium Richard (PC; isotype, PC!).

UNITED STATES—ALABAMA. Blount Co.—Cullman, Kral 26659 (VDB). Dale Co.—Brandidge, Gonsoulin 1226 (NY, PH, SMU, US, VDB). Geneva Co.—Sampson, McDaniel 8924 (FSU, VDB). Lee Co.—Auburn, Baker 6438 (MO, NY, UC), Earle & Baker, 4 Apr 1893 (F, GH, MO, NY).

ARKANSAS. Ashley Co.—Hamburg, Demaree 14705 (GH, MO, NY, SMU). Cross Co.—McDonald, Gonsoulin 1043 (NY, PH, SMU, US, VDB). Desha Co.—Pendleton, Gonsoulin 1040 (NY, PU, SMU, US, VDB). Drew Co.—Monticello, Demaree 13673 (GH, MO, NY). Perry Co.—Nimrod, Demaree 46444 (DUKE, SMU).

DISTRICT OF COLUMBIA. Washington, L. Ward, 24 May 1881 (GH), G. Vasey (F).

FLORIDA. Calhoun Co.—Blountstown, McDaniel 8744 (FSU, VDB). Dixie Co.—Cross City, Small, 25 Apr 1921 (GH, NY, UNC). Gadsden Co.—River Junction, Harbison 1485 (GH, UNC). Levy Co.—Otter Springs, Kral 4089 (FSU, SMU, UNC, VDB). Okaloosa Co. Laurel Hill, Godfrey 61624 (FSU, SMU).

GEORGIA. Baldwin Co.—Milledgeville, Harbison 1550 (GH, UNC). Charlton Co.—Mattox, Gonsoulin 1233 (NY, PH, SMU, US, VDB). Crisp Co.—Cordele, Moore & Lauren 664 (FSU, GA). Dougherty Co.—Albany, Gillspie 4972 (GH, SMU, UC). Gwinnett Co.—McGuires Mill, Small, 7 May 1895 (F, GH, NY).

ILLINOIS. Alexander Co.—Cache, Palmer 14935 (GH, MO). Johnson Co.—Grantsburg, Winterringer 1951 (TEX). Massac Co.—Metropolis, Gleason 2554 (GH). Pope Co.—Golconda, Bauer, 31 May 1940 (F). Pulaski Co.—Karnak, Palmer 15119 (GH).

INDIANA. Huntington Co.—Huntington College, Henderson, 5 May 1959 (FSU). Lake Co.—Schnieder, Deam 36493 (GH). La Porte Co.—La Cross, Deam 38780 (GH, PH). Porter Co.—Baum Bridge, Deam 34864 (GH, NY). Posey Co.—Mt. Vernon, Hermann 6671 (F, NY).

KENTUCKY. Marshall Co.—McCoy, 5 Jul 1939 (UC). Muhlenberg Co.—Price 2118 (MO). Union Co.—Caney Mound School, Shacklette 346 (GH, NY).

LOUISIANA. Avoyelles Par.—Marksville, *Gonsoulin* 1035 (NY, PH, SMU, US, VDB). Caldwell Par.—Columbia, *Thomas & Gilliam* 2934 (LAF, UNC). Iberia Par.—Weeks Island, *Thieret* 17065 (DUKE, FSU, LAF, TEX). Livingston Par.—Georgeville, *Thieret* 27117 (DUKE, FSU, LAF). Ouachita Par.—Cheniere, *Kral* 20036 (VDB).

MISSISSIPPI. Calhoun Co.—Skuna River, *Gonsoulin* 1028 (NY, PH, SMU, US, VDB). Harrison Co.—Harrison, *Jones* 14722 (SMU, TEX). Handsboro, *Demaree* 32507 (SMU, UNC, VDB). Jackson Co.—Ocean Springs, *Skehan*, 22 Apr 1895 (GH, MO, UC). Lamar Co.—Purvis, *Jones* 7982 (GA, GH, FSU, UNC).

MISSOURI. Butler Co.—Neelyville, *Eggert*, 8 Aug 1893 (F, GH, NY, UC), *Redfearn & Eggers* 14538 (FSU, GA, UNC, LAF). Dunkin Co.—Campbell, *Cunningham*, 20 Jun 1934 (GH). Piproly Co.—Naylor, *Palmer & Steyermark* 41574 (MO, NY, PH). Stoddard Co.—Advance, *Steyermark* 20835 (MO).

NORTH CAROLINA. Bladen Co.—Clarkston, *Gonsoulin* 1123 (NY, PH, SMU, US, VDB). Buncombe Co.—Biltmore, 4669a (GH, MO, NY). Cumberland Co.—Fayetteville, *Holmes*, 13 Apr 1921 (FSU, UNC). Gates Co.—Chowan R., *Fernald* 11605 (DUKE, GH); Camels Creek, *Radford* 5678 (GH, UNC). Johnston Co.—Smithfield, *Radford & Stewart*, 200 (NY, SMU, UC, UNC).

PENNSYLVANIA. Lancaster Co.—Lancaster, *Small*, Jul 1889 (F).

SOUTH CAROLINA. Anderson Co.—Tugaloo R., *Radford* 12067 (GA, GH, NY, UNC, VDB). Beauford Co.—Buffton, *Millichamp*, Apr 1880 (GH, MO, NY). Berkeley Co.—Santee R., *Little & Wood* 14314 (UNC); Bonneau, *Godfrey* 478 (GH, F, MO, NY, UC). Chesterfield Co.—Bay Forest, *Radford* 12304 (UC, UNC).

TENNESSEE. Hamilton Co.—Chicamauga Lake, *Gonsoulin* 1242 (NY, PH, SMU, US, VDB). Haywood Co.—Shepard, *Palmer* 17473 (GH, MO). Madison Co.—Jackson, *Bain* 133 (NY, UNC). Obion Co.—Troy, *Fairchild* 8387 (GA); Obion, *Sharp* 7853 (DUKE, FSU, GH, NY, SMU, TEX, UNC, UC).

TEXAS. Jasper Co.—Jasper, *Correll* 15337 (FSU, UNC). Liberty Co.—Doleu Swamp, *Young*, 21 Apr 1914 (TEX). Marion Co.—Smithland, *Correll*, 29 Jul 1967 (UC). Newton Co.—Allen 39050 (TEX). Polk Co.—(collector unknown) 4670, 27 Apr 1903 (NY). San Augustine Co.—San Augustine, *Palmer* 13256 (GH, MO).

VIRGINIA. Charles City Co.—Chickahominy River, *Fernald* 13391 (GH). Henrico Co.—Elke Station, *Fernald* 9394 (F, GH, MO). Isle of Wright Co.—Joiners Bridge, *Harvill* 13847 (SMU, UNC). Southampton Co.—Franklyn, *Fernald* 10780 (F, GH, MO). Sussex Co.—Kello's Dam, *Fernald* 14951 (GH).

Styrax americana is a well-marked species not easily confused with the sympatric *S. grandifolia*. However, there exists a considerable range of morphological variation between *S. americana* and var. *pulverulenta*. Characters separating the two are based on a difference in pubescence on the lower surface of the leaves, on the pedicels, on the calices, and on new shoot growth. Also used is the length of the pedicels, var. *americana* having a much larger pedicel-calyx ratio. The two are often found growing in the same

habitat, although var. *pulverulenta* is more often found on higher, slightly more sandy soils than is var. *americana*. Variety *pulverulenta* is slightly more southern in its range, reaching a northernmost extension in central Arkansas eastward. These two taxa seem to be hybridizing and backcrossing wherever their habitats overlap. Intermediates are often more numerous than either of the two well-defined varieties, and positive identification may be impossible. The leaves on any specimen of "good" var. *americana* are glabrous and larger than those of a "good" *pulverulenta* in addition to being toothed toward the apices. Leaves of the latter variety are smaller than those of the former and are densely scurfy-hairy on the undersurfaces and petioles. In addition, var. *pulverulenta* has pedicels barely if at all longer than the calices, and these are also densely scurfy-hairy. This is in contrast to the long, glabrous pedicels of var. *americana*. In areas where the two varieties overlap the characters used in their definition are absent or possessed to various degrees; that is, the states of the characters differ for different specimens. To solve this problem I employed series of characters, each weighted equally in a manner similar to that used in numerical taxonomy. This method offers the best solution for defining the two varieties in the areas of overlap, although as expected there are some specimens that remain doubtful.

1b. *STYRAX AMERICANA* Lamarck var. *PULVERULENTA* (Michaux) Rehder, Bailey Stand. Cycl. Hort. 6:3280. 1917.

Styrax pulverulentum Michx., Fl. Bor.-Amer. 2:41. 1803.

Styrax americanum fma. *pulverulentum* (Michx.) Perkins, Pflanzenreich IV. 241 (Heft 30): 76. 1907.

Leaf blades elliptical to oval, ovate or obovate, 2–10 cm long; upper surfaces dark green, glabrous or with a few scattered trichomes near the veins; lower surfaces paler, finely to densely scurfy-hairy to tomentose; petioles 3–5 mm long, densely pubescent. Pedicels 4–6 mm long, densely scurfy-hairy; calices pale, 3–4 mm long, densely to moderately pubescent, teeth small, acute; corolla lobes 8–10 mm long, elliptic-oblong or lanceolate-oblong, lightly soft downy pubescent (Fig. 3).

Styrax americana var. *pulverulenta* generally occupies slightly drier, better-drained alluvial soils than does var. *americana*. It is, however, found in very wet sites growing near the latter species, hybridizing and backcrossing with it. It ranges from South Carolina, south throughout Florida, and westward along the Gulf Coast, and into eastern Texas, then north into Arkansas and southern Missouri (Fig. 17).

The usual flowering time for var. *pulverulenta* is April through May, but, as does var. *americana*, it exhibits seasonal variation. The colloquial name is "Downy American snow-bell."

Holotype: U.S.A. CAROLINAS. Michaux. Herbarium Richard (PC; isotype: PC!).

UNITED STATES. ALABAMA. Baldwin Co.—Morgan, *Iltis* 25441 (UNC, UC). Butler Co.—McKenzie, *Henry* 5725 (PH). Covington Co.—McRae, *Hen-*

ry 3331 (PH). Escambia Co.—Lindsey, *Gaines* 294 (GA, NY). Houston Co.—Cottonwood, *Kral* 31322 (VDB). Mobile Co.—Theodore, *Kral* 28313 (VDB).

ARKANSAS. Arkansas Co.—Gillette, *Demaree* 21058 (GH, MO, NY, SMU, UC). Clay Co.—Corning, *Letterman*, 10 Sep. 1883 (MO). Drew Co.—Wilmar, *Demaree* 24714 (SMU). Garland Co.—Ashe, 22 May 1931 (UNC). Hempsted Co.—Fulton, *Letterman*, 7 May 1884 (GH). Hot Springs Co.—Malvern, *Demaree* 14784 (SMU). Lafayette Co.—Lewisville, *Fisher* (SMU). Miller Co.—Doddridge, *Demaree* 40817 (FSU, SMU). Mississippi Co.—Osceola, *Demaree* 4265 (MO). Nevada Co.—Bluff City, *Demaree* 48150 (UNC, VDB), *Demaree* 60084 (VDB). Prairie Co.—Hagen, *Demaree* 67808 (VDB), 57627 (VDB). Sevier Co.—Altis, *Brinkley* 237 (F, TEX).

FLORIDA. Baker Co.—McClenny, *Lighthipe*, Apr 1899 (TEX). Bradford Co.—Lawtry, *Murrill*, 24 Apr 1940 (DUKE, MO). Charlotte Co.—Punta Gorda, *Small*, 27 Apr 1923 (DUKE). Clay Co.—Cove Springs, *Rau*, 21 Mar 1884 (PH). DeSoto Co.—Arcadia, *Oosting* 182 (DUKE). Duval Co.—Jacksonville, *Curtiss* 1768 (F, GH, GA, MO, NY). Escambia Co.—Perdido R., *Ripley* 10121 (NY). Franklyn Co.—Apalachicola R., *Sargent*, 15 Mar 1891 (GH). Gadsden Co.—Midway, *Godfrey* 61920 (FSU, SMU, UNC, UC, VDB). Gulf Co.—Wewahitchka, *Henry* 1505 (PH). Holmes Co.—Bonifay, *Leeds* 2422 (PH). Jackson Co.—Cottondale, *Harbison*, 29 May 1916 (GH). Jefferson Co.—Waukeenah, *Eyles* 8262 (GA). Leon Co.—Tallahassee, *Kral* 6382 (GH, UC, USL, VDB). Manta Co.—Miacca, *Smith*, 4 Mar 1904 (PH). Manatee Co.—Webb, 1887 (F). Okaloosa Co.—Baker, *Henry* 3752 (PH). Santa Rosa Co.—Milton, *McDaniel* 4868 (FSU, VDB). Sarasota Co.—Osprey, *Smith* 914-271 (DUKE). St. Johns Co.—St. Johns R., *Curtiss* 1768 (GA, F, PH, UC). Wakulla Co.—Ashe, 28 Jul 1928 (UNC). Walton Co.—Seagrove Beach, *Schuster* A-7324 (DUKE, VDB).

GEORGIA. Brooks Co.—Quitman, *Pyron* 2179 (GA). Bullock Co.—Statesboro, *Bailey* 80 (GH). Irwin Co.—Irwin, *Plummer* 182 (GA). Liberty Co.—Taylor Creek, *Duncan* 2231 (GA). Randolph Co.—Cuthbert, *Henry* 1891 (PH). Tattnall Co.—Glennville, *Padget* 230 (GA). Thomas Co.—Coolidge, *Godfrey* 69463 (FSU, UNC). Tombs Co.—Lyons, *Plummer* 162 (GA). Ware Co.—Waycross, *Williamson*, Apr 1897 (PH). Wayne Co.—Jessup, *Harvey*, 9 May 1940 (GA). Worth Co.—Sylvester, *Thorne* 6330 (GA).

LOUISIANA. Allen Par.—Kinder, *Thieret* 18712 (LAF). Caddo Par.—Vivian, *Thieret* 27606 (LAF). Caldwell Par.—Columbia, *Thieret* 20780 (LAF). Natchitoches Par.—*Harbison*, 5 Jul 1930 (UNC). Orleans Par.—Lake Pontchartrain, *Small*, 21 Apr 1928 (NY). Ouachita Par.—Lake Cheniere, *Kral* 8862 (FSU, LAF, UNC). Rapides Par.—Alexandria, *Hale* (F, PH). Sabine Par.—Many, *Demaree* 47369 (UNC); Toro, *Demaree* 48234 (UNC). Tangipahoa Par.—Hammond, *Cooley* 4176 (GA). Union Par.—Farmerville, *Henry* 6429 (PH).

MISSISSIPPI. Franklin Co.—Eggert, 6 May 1893 (UNC). Jackson Co.—Ocean Springs, *Earle*, 29 Apr 1889 (NY), *Skehan* 99 (DUKE, GH, F, MO, TEX, UNC, SMU).

MISSOURI. Butler Co.—Neelyville, *Steyermark* 26616 (F).

SOUTH CAROLINA. Berkeley Co.—Wando, *Duncan* 5989 (GA). Williams-

burg Co.—Greeleyville, *Radford* 21313 (UNC).

TEXAS. Angelina Co.—Nacogdoches, *Cory* 26001 (GH). Cass Co.—Cass, *Gentry* 3478 (UNC). Gregg Co.—York, 24 Jul 1939 (GH). Hardin Co.—Silsbee, *Palmer* 9578 (GH, MO). Harrison Co.—Taylors Island, *Whitehouse* 30348 (SMU). Jefferson Co.—Beaumont, *Reverchon* 3869 (GH, MO). Marion Co.—Smithland, *Correll* 38479 (UNC). Nacogdoches Co.—Nacogdoches, *Waller* 179 (TEX). Newton Co.—Deweyville, *Whitehouse* 30143 (SMU). Orange Co.—*Letterman*, Aug 1880 (MO). Polk Co.—Tharp, 15 May 1942 (TEX). Tyler Co.—Chester, *Tharp* 54773 (SMU, TEX). Upshur Co.—Ore City, *Correll* 13181 (NY, SMU).

This taxon was first described by Michaux (1803) and was given the rank of species. It was later lowered to the rank of forma by Perkins (1907) and then raised to varietal rank by Rehder (1917). In this treatment I am following Rehder's designation because I believe that the characters separating it from var. *americana* are not sufficient to justify recognizing it as a species. As mentioned previously, intermediates difficult if not impossible to identify do occur, but the identity of the variety and the species remains distinct.

Variety *pulverulenta*, being densely scurfy hairy, is often confused with *S. grandifolia*. The leaves of the latter species are obovate and usually quite large, but sometimes on high dry sites, they are much smaller and are barely if at all obovate, being more ovate. It is this form of *S. grandifolia* with which var. *pulverulenta* is confused and then only when flowering or fruiting material is not available.

2. *STYRAX GRANDIFOLIA* Aiton, Hort. Kew. 2:75. 1789.

Styrax officinalis sensu Walt., Fl. Carol. 140. 1788 (non L., 1753).

Styrax cavaleriei Lév., Repert. Spec. Nov. Regni Veg. 4:331. 1907.

Styrax touchanensis Lév., op. cit. 11:64. 1912.

Broad shrub to small tree, to 9 m high, the branching somewhat flabellate but forming a roundish crown. Leaf blades obovate, oval-elliptic, 4–20 cm long, margins distantly toothed or entire, the bases cuneately narrowed or rounded, apices acute to short acuminate; upper surfaces glabrous, varying from pale to dark green; lower surfaces densely to finely tomentose, pale; petioles 4–9 mm long, pubescent. Flowers solitary, or more often in loose, axillary, drooping, 5–20 flowered racemes, 5–15 cm long, subtended by small bracts; calices 4–5 mm long, canescent, teeth small, acute; corolla lobes 15–22 mm long, elliptic, soft downy pubescent, apices acute to rounded; stamens as long as corolla lobes; filaments densely pilose at base to 1/3 their length; anthers 1/3 the length of the stamens; style about 2 mm longer than the stamens; stigma 3-lobed. Drupes subglobose, 7–9 mm in diameter, lightly tomentose, portion of the style persistent as an apiculation; seeds 1–2, globose or ovoid, dark brown, dull (Fig. 4).

Styrax grandifolia occupies a variety of sites from low woods to higher well-drained sandy soils, upon which it is probably more prevalent. It ranges throughout the southeastern United States from Virginia to southern Florida, westward through Louisiana (although it is scarce in the coastal marshes,

occurring there only on raised ridges such as salt domes, etc.), and into eastern Texas, then northward to southeastern Missouri (Fig. 17).

The flowers appear with the leaves from March through April. The colloquial name is "Big leaf snow-bell."

Holotype: U.S.A. *Hort. Fothergill*, 1779 (BM; photograph of holotype examined. A representative specimen of *S. grandifolia*, sent to BM, was found to represent the same species as the holotype).

UNITED STATES. ALABAMA. Cherokee Co.—Little River, *Kral* 33355 (VDB). Choctaw Co.—Nanafalia, *Gonsoulin* 1029 (NY, PH, SMU, US, VDB). Cullman Co.—St. Bernard, *Germann*, 12 May 1930 (GH, F, NY, UC). Franklin Co.—Bear Creek, *Kral* 26448 (VDB). Marengo Co.—Magnolia, *Clark* 13770 (UNC).

ARKANSAS. Conway Co.—Morrilton, *Demaree* 45521 (SMU, VDB). Hot Springs Co.—Malvern, *Demaree* 56562 (SMU, VDB). Madison Co.—Brashers, *Gonsoulin* 1010 (NY, PH, SMU, US, VDB). Pulaski Co.—Pinnade, *Demaree* 8882 (GH, NY, SMU). Saline Co.—Paron, *Demaree* 59891 (VDB).

FLORIDA. Calhoun Co.—Altha, *Godfrey* 52702 (FSU, UNC, VDB). Duval Co.—Jacksonville, *Curtis* 6357 (MO, NY, SMU, UC). Jackson Co.—Chipola R., *Godfrey* 57722 (GH, FSU). Taylor Co.—Athena, *Gonsoulin* 1229 (NY, PH, SMU, US, VDB). Walton Co.—Eucheena, *Godfrey* 62684 (FSU, SMU, UNC, VDB).

GEORGIA. Bartow Co.—Allatoona R., *Duncan* 8095 (GA, MO). Ben Hill Co.—Abbeville, *Wilbur* 3067 (FSU, GA). Bullock Co.—Statesboro, *Ahles* 1145 (GH, SMU). Colquitt Co.—Ellenton, *Gonsoulin* 1234 (NY, PH, SMU, US, VDB). Early Co.—Hilton, *Thorne* 5356 (F, GH, NY). Lee Co.—Starksville, *Duncan* 2324 (GA, UNC).

KENTUCKY. Clay Co.—Spurlock, *Gonsoulin* 1204 (NY, PH, SMU, US, VDB). Harrison Co.—Cynthiana, *Gonsoulin* 1206 (NY, PH, SMU, US, VDB).

LOUISIANA. Acadia Par.—Eunice, *Gonsoulin* 1003 (NY, PH, SMU, US, VDB). Avoyelles Par.—Ringgold, *Ewan* 18985 (GA, GH, MO). Catahoula Par.—Harrisonburg, *Thieret* 28749 (FSU). Lincoln Par.—Vienna, *Thieret* 24534 (LAF, UNC). Ouachita Par.—Monroe, *Kral* 8532 (FSU, GH, SMU).

MISSISSIPPI. Clarke Co.—Quitman, *Jones* 12058 (GA, FSU). Forest Co.—Hattisburg, *Harbison* 15743 (GH, UNC). George Co.—Lucedale, *Gonsoulin* 1016 (NY, PH, SMU, US, VDB). Lauderdale Co.—Mt. Barton, *Jones* 7037 (GA, FSU, UNC). Tallahatchie Co.—Charleston, *Hardin* 15420 (GA).

MISSOURI. New Madrid Co.—La Forge, *Steyermark* 69683 (F).

NORTH CAROLINA. Bladen Co.—Elizabethtown, *Ahles* 23495 (GA, NY, UNC, VDB). Craven Co.—Fort Barnwell, *Totten*, 27 May 1958 (UNC). Guilford Co.—Deep River, *Melvin*, 20 Sep 1953 (UNC). Lee Co.—Moncure, *Radford* 6272 (GH, UNC). Stanly Co.—Yadkin R., *Palmer* 39989 (GH, MO).

SOUTH CAROLINA. Abbeyville Co.—Abbeville, *Radford* 22816 (FSU, UNC). Beauford Co.—Beauford, *Millichamp* 1883 (F, NY, UNC). Chesterfield Co.—McBee, *Gonsoulin* 1121 (NY, PH, SMU, US, VDB). McCormick Co.—McCormick, *Duncan* 10989 (GA, MO). Oconee Co.—Walhalla, *Huger*, May

1895 (NY, PH, SMU, US, VDB).

TENNESSEE. Cumberland Co.—Linary, *Gonsoulin* 1116 (NY, PH, SMU, US, VDB). Decatur Co.—Sugartree, *Sharp* 12916 (DUKE, FSU, GA, GH, MO, NY, SMU, UNC). Hickman Co.—Vernon, *Shanks* 5854 (GA). Marion Co.—Gizzard Cove, *Ramseur* 1133A (UNC). Wayne Co.—Waynesboro, *Kral* 31681 (VDB).

TEXAS. Angelina Co.—Zavalla, *Gonsoulin* 1007 (NY, PH, SMU, US, VDB). Hardin Co.—Silsbee, *Cory* 52764 (NY, SMU). Jasper Co.—Jasper, *Correll* 27425 (UNC), *Correll* 29106. Newton Co.—Newton, *Cory* 52647 (SMU). Sabine Co.—Hemphill, *Quarterman* 58-80 (VDB). Tyler Co.—Woodville, *Kral* 29119 (VDB).

VIRGINIA. Bath Co.—Clifton, *Gonsoulin* 1129 (NY, PH, SMU, US, VDB). Nansemond Co.—Suffolk, *Bartram*, 17 Sep 1907 (PH).

This species is well marked. Within its range there is no species of *Styrax* with which it can be confused. Earliest records of *S. grandifolia* appear in Walter's *Flora Caroliniana* (1788). Walter referred to the material he studied as *S. officinalis* L. Aiton (1789) corrected this misidentification by applying the name *S. grandifolia* Ait. The original description given by Aiton is rather brief, but the geographic area occupied by this species does not allow for error.

There seems to be much variation in this species, which may explain why Walter thought he was dealing with *S. officinalis* instead of a new species.

The leaves of *S. officinalis*, both of the Mediterranean species and of the two Californian varieties, are broadly elliptic to nearly orbicular and are 4–8 cm long, in comparison with those of *S. grandifolia*, which are generally obovate and are 6–20 cm long. The lower surface of the leaf of the former varies from glabrous to fulvescent, depending on the variety.

However, many times when *S. grandifolia* is growing on high, well-drained, sandy soils, the mature leaves are 4–8 cm long (unusually small) and are often nearly orbicular shape as in *S. officinalis*. Although the flowers of *S. officinalis* are larger than those of *S. grandifolia*, a mistake in identity could easily be made.

Styrax grandifolia shares its geographic range with another well-marked species, *S. americana*, but the two rarely overlap in their ecological ranges, because *S. americana* occupies lower moister sites.

3. STYRAX PLATANIFOLIA Engelmann

Key to Varieties

- 1a. Leaves essentially glabrous; pedicels glabrous or nearly so; calices glabrous or covered with a light matted pubescence; distribution centering about Llano County, Texas (Fig. 5). . . 3a. *S. platanifolia* var. *platanifolia*
- 1b. Leaves bearing scattered coarse stellate trichomes; pedicels and calices covered with a dense fine indumentum; distribution centering around Bandera and Kendall Counties, Texas (Fig. 5).

. . . 3b. *S. platanifolia* var. *stellata*

3a. *STYRAX PLATANIFOLIA* Engelmann var. *PLATANIFOLIA*, Boston J. Nat. Hist. 6:146-147. 1854.

Shrub to 4 m with freely branched, open, irregular crown and rather slender branchlets. Leaves glabrous, suborbicular, blades 3-8 cm long, margins entire, undulate, or angulate toothed, the bases broadly subcordate or truncate, apices acute to obtuse; upper surfaces light to dark green, semilustrous; lower surfaces paler; veins finely reticulate on both surfaces; petioles slender, 3-13 mm long, glabrous or very faintly pubescent. Flowers in axillary, semi-drooping, 3-5 flowered racemes, 3.5-7 cm long, subtended by minute bracts; pedicels 6-10 mm long, slightly pubescent; calices 4-6 mm long, semiglabrous, campanulate, truncate, shallowly toothed, teeth acute; corolla lobes 12-14 mm long, oblong to elliptic or ovate, apex obtuse to acute, surface with soft downy pubescence; stamens just shorter than corolla lobes; filaments flattened, pubescent near base; style exserted, slightly longer than the stamens, pubescent $\frac{1}{2}$ way to apex; stigma barely 3-lobed. Drupes subglobose or ovate, 8-10 mm in diameter, style persistent as an apiculation; seeds 1-2, oval to ovate, rounded at the apex and base with a ridge running from the hilum sideward (Fig. 5).

Styrax platanifolia occurs in rather dry, wooded bottomlands and on rocky banks and ledges in central Texas in the Edwards Plateau region (Fig. 18).

The flowers appear with the leaves from early March through April. The colloquial name is "Sycamore-leaf snow-bell."

Holotype: U.S.A. TEXAS. Comal Co.: Near New Braunfels. *Lindheimer*, Mar 1852 (MO!).

UNITED STATES. TEXAS. Blanco Co.—Twin Sisters, *Gonsoulin* 1289 (NY, PH, SMU, US, VDB); Fishers Store, Parks S.N. (SMU, TEX); Little Blanco R., Parks, 24 Aug 1947 (SMU); Blanco, *Henry* 6523 (PH), *Wilson* T-41 (F). Burnet Co.—Bertram, *Tharp*, 16 Jun 1950 (TEX), *Carsner* (SMU); Smithwick, *Henry* 6557 (PH). Caldwell Co.—Delhi, *Gonsoulin* 1287 (NY, PH, SMU, US, VDB). Comal Co. New Braunfels *Lindheimer*, Mar 1852 (GH). Edwards Co.—Rocksprings, *Gonsoulin* 1306 (NY, PH, SMU, US, VDB). Gillespie Co.—Enchanted Rock, *Jermy* 105 (F, MO). Hays Co.—Cedar Park, *Gonsoulin* 1288 (NY, PH, SMU, US, VDB); San Marcos, *Stanfield* 1897 (NY). Kerr Co.—Hunt, *Gonsoulin* 1305 (NY, PH, SMU, US, VDB). Kimble Co.—*Palmer* 10709 (GH, MO); Big Joline Creek, *Reverchon*, May 1885 (GH), *Coleman*, 18 May 1960 (TEX). Kendall Co.—Boerne, *Palmer* 9843 (MO, PH); Curry Creek, *Correll* 29152 (UNC); Kendalia, *Correll* 29572 (UNC); Spanish Pass, *Clemens*, 5 Jul 1911 (F). Kinney Co.—Laguna, *Gonsoulin* 1307 (NY, PH, SMU, US, VDB). Llano Co.—Enchanted Rock, *Whitehouse*, 12 Jun 1930 (GH, MO, NY, UNC), C.C.A. (TEX). Real Co.—Leakey, *Gonsoulin* 1307 (NY, PH, SMU, US, VDB). Travis Co.—Cow Creek, *Correll* 37003 (FSU, UNC); Austin, *Whitehouse*, 3 May 1930 (GH, MO, SMU), *Prowse*, 3 May 1930 (TEX), *Huppertz*, Apr 1913 (TEX), *Wright* (GH); Bull Creek, *Young*, 19 Apr 1910 (MO, TEX).

Styrax platanifolia var. *platanifolia* occurs in the Edwards Plateau region of Texas. The upper or western edge of the Coastal Plain lies at an elevation

of about 600 ft., and the escarpment of the Edwards Plateau to the west rises to an average elevation of 2,700 ft. The various drainage courses descend from the plateau to the Coastal Plain through canyons. *Styrax* occurs only on the escarpment and in the canyons.

Styrax platanifolia var. *platanifolia* is described as having the foliage, pedicels, and calices glabrous or nearly so. This characterization is accurate for specimens from the northern and eastern portions of the range. However, in the southern and southwestern portions it grades into var. *stellata*, the intermediates having varying amounts of pubescence. Both var. *platanifolia* and var. *stellata* grow on highly calcareous soils and at elevations of a few hundred feet or lower.

There seems to be no confusion in the earlier literature as to the identity of this species. *Styrax platanifolia* was the only *Styrax* reported in central Texas and none was known from western Texas. However, Cory (1943) described a new variety, *S. platanifolia* var. *stellata*, and two new species, *S. texana*, whose range overlaps that of *S. platanifolia*, and *S. youngae*, from the Davis Mountains in western Texas. He summarized the differences among the three species of western Texas *Styrax* as follows:

<i>S. platanifolia</i>	<i>S. texana</i>	<i>S. youngae</i>
Upper leaf surface dull green, glabrous to bearing scattered stellate trichomes; reticulate veiny.	Upper leaf surface bright green, glabrous, not reticulate veiny.	Upper surface dull green, densely and coarsely stellate pubescent, not reticulate veiny.
Lower and upper leaf surfaces similar.	Lower surfaces markedly dissimilar to upper, lower bright silvery with a fine and dense indumentum only.	Lower dissimilar to upper but not markedly so; grayish tomentose with a fine and dense indumentum beset with coarse stellate hairs.
Pedicel glabrous or nearly so.	Pedicel pubescent.	Pedicel densely coarsely stellate pubescent.
Calyx dark brown, glabrous to finely puberulent; apex glandular and prominently toothed.	Calyx pale, densely puberulent; apex glandular and prominently toothed.	Calyx dark brown, densely stellate pubescent; apex non-glandular, the teeth inconspicuous.
Style pubescent half-way to apex.	Style pubescent only at base.	Style pubescent nearly to apex.

Styrax platanifolia is easily distinguished from *S. texana* and *S. youngae* by its larger more reticulate-veiny leaves. The glandular, prominently-toothed calices of *S. texana* are reliable in separating it from *S. youngae*, which has non-glandular inconspicuous teeth. The above chart together with ecological information should make identification quite easy.

My collections of *S. platanifolia* in 1969 added several new counties to its known range. All the plants of these collections were growing on rocky ledges, slopes, or other well-drained areas.

3b. *STYRAX PLATANIFOLIA* Engelmann var. *STELLATA* Cory, Madroño 7(4): 111-112. 1943.

Upper surfaces of the leaves dull green with scattered stellate trichomes; lower surfaces pale, covered with coarse stellate trichomes. Veins numerous and finely reticulate on both surfaces; petiole slender, 8-13 mm long, very faintly pubescent. Pedicels 6-10 mm long, covered with a dense fine indumentum; calices 4-6 mm long, covered with a dense fine indumentum (Fig. 5).

Styrax platanifolia var. *stellata* occurs in the Edwards Plateau region of Texas centering in Bandera and Kendall counties, extending into Bexar and Guadalupe counties. Through its range it occurs on the same type wooded bottomlands, rocky banks, and ledges as var. *platanifolia* (Fig. 18).

The flowers appear from early March through April. The colloquial name is "Hairy sycamore-leaf snow-bell."

Holotype: U.S.A. TEXAS. Bandera Co.: 6.5 miles north of Vanderpool. Cory, 16 Jun 1940 (TEX! isotypes: F! NY!).

UNITED STATES. TEXAS. Bandera Co.—Vanderpool, Cory, 15 Jun 1940 (GH), Cory 49452 (SMU), Cory 34764 (F, TEX, NY), Henry 6539 (SMU), Palmer 11528 (MO, NY), Parks 1009 (GH), Parks 40990 (GH, TEX); west of Boerne, Johnson 599 (TEX); Seco Creek, Palmer 10237 (GH). Bexar Co.—Leon Springs, Cappell T316 (FSU). Guadalupe Co.—Cibolo, Schattenbert, 15 Jun 1913 (GH). Kendall Co.—Boerne, Hastings, 1911 (GH), Palmer 9843 (GH); Cebolo Creek, Palmer 11474 (GH, MO, NY); Spanish Pass, Clemens, 5 Jul 1911 (MO, TEX).

4. *STYRAX TEXANA* Cory, Madroño 7(4): 112-113. 1943.

Spreading shrub, 1.5-4 m high, with slender irregular branches. Leaves oval to broadly elliptic, blades 4-8 cm long, about as broad, margins entire or subentire, the bases truncate or rounded, apices abruptly acute or blunt-pointed; upper surface bright green, smooth, glabrous; lower surfaces conspicuously white with dense indumentum, veins prominent; petioles 8-15 mm long, green to reddish, grooved above, with scattered trichomes. Flowers axillary, solitary, or in 2-5 flowered racemes, 12-20 mm long, subtended by minute bracts; pedicels 10-12 mm long, puberulent; calices 4-6 mm long, pale, densely puberulent, apex glandular and 5-7 toothed; corolla lobes 14-18 mm long, elliptic to oblong, puberulent, apex obtuse to acute; stamens as long as corolla lobes; filaments flattened, pubescent near the base; style stout at the base, pubescent only at the base, often exceeding the length of

the corolla lobes; stigma slightly lobed. Drupes maturing August–September, globose to subglobose, 7–8 mm in diameter, style barely persistent as a small apiculation; seeds 1–2, globose, smooth, often with one or two shallow grooves on the sides (Fig. 6).

Styrax texana is confined to central Texas where it usually grows in inaccessible places on steep limestone cliffs, generally at elevations just below 2,000 ft. The type locality is Edwards County. In addition, it occurs in Bexar and Real counties (Fig. 18).

The flowers appear with the leaves in mid-April. The colloquial name is "Texas snow-bell."

Holotype: U.S.A. TEXAS. Edwards Co.: Polecat Canyon. Cory, 19 Apr 1942 (GH! isotypes: GH! NY!).

UNITED STATES. TEXAS. Bexar Co.—Nueces Canyon, Cory 42659 (F), Cory 42678 (F). Edwards Co.—Polecat Creek, Cory 34940 (GH), Cory 34936 (SMU, TEX), Cory 38939 (GH, NY), Cory 38935 (TEX), Cory 49178 (SMU); Cedar Creek, Cory 37767 (TEX), Cory 38763 (TEX); Little Hackberry Creek, Cory 42955 (SMU, TEX), Cory 42953 (NY). Real Co.—Nueces River, Cory 42677 (NY, TEX), Cory 42661 (NY), Cory 42664 (NY), Cory 42873 (GH), Cory 42668 (GH).

This species occurs with *S. platanifolia* and its var. *stellata* in the southwestern part of their range. The foliage of *S. platanifolia* is usually of larger dull green leaves with a coarse texture, being distinctly reticulate veiny, and undulate or angulate toothed. The foliage of *S. texana* is much finer in texture, with the upper leaf surface dark green in contrast to the lower surface, which is bright silvery with a very dense, fine, silky, pubescence; neither surface is distinctly reticulate veiny.

The calyx and pedicel of *S. texana* are densely puberulent while those of *S. platanifolia* are glabrous or nearly so, as in var. *stellata*. The apex of the calyx in *S. texana* is glandular and is prominently toothed, two characters which help to distinguish it from *S. youngae*, also of southwestern Texas (see discussion under *S. platanifolia* for character comparisons).

5. *STYRAX YOUNGAE* Cory, Madroño 7(4): 113-115. 1943.

Shrub, 2.5–3 m high. Leaves orbicular to elliptical, blades 2.5–5 cm long, to 3.5 cm broad, margins entire or subentire, bases more or less rounded, apices acute; upper surface dark green, with coarse stellate hairs, not reticulate veiny; lower surfaces tomentose, but not silvery, with very fine and dense indumentum of coarse stellate hairs, veins prominent, straw colored; petiole 5–6 mm long, tomentose. Flowers in axillary, 3–7 flowered racemes, 4–20 mm long, coarsely stellate pubescent; pedicels stout, 4–8 mm long, densely and coarsely stellate pubescent; calices 4–5 mm long and broad, dark brown, densely stellate pubescent, apex truncate, non-glandular, teeth inconspicuous; corolla lobes 12–15 mm long, narrowly elliptic, obtuse, densely stellate puberulent; style stout, 16–17 mm long, stellate pubescent to near the apex; stigma barely lobed. Drupes globose, 8–10 mm in diameter; seed 1, subglobose, smooth (Fig. 6).

Until now, the type collection, from a canyon in the Davis Mountains, Texas, was the only one available for this species. However, two unidentified collections of *Styrax* I examined during my study turned out to be *S. youngae*. These were from Coahuila and Nuevo León, Mexico, thus extending the known range of this species (Fig. 18).

The flowers appear from April through May. The colloquial name is "Young's snow-bell."

Holotype: U.S.A. TEXAS. Davis Mountains, canyon. Young, 12 May 1914 (TEX!).

MEXICO. COAHUILA. Rancho Auga Dulci, Wynd & Mueller 340 (GH, MO, NY).

NUEVO LEON. Monterrey, Smith M149 (TEX).

UNITED STATES. TEXAS. Davis Mts., Young, 12 May 1914 (TEX); Limia Canyon, Young 23 (MO).

The type collection of *S. youngae* is the only collection of *Styrax* from the mountains of southwestern Texas. The exact type locality is unknown but Cory (1943) states "it is likely some minor canyon for the larger ones are named and were known even more than 30 years ago." The species is named after its discoverer, a pioneer botanist in exploration of the mountains of southwestern Texas.

Styrax youngae grows in soils developed on igneous rocks and in which free limestone is absent, at elevations in excess of 4,000 ft. *Styrax texana* grows at elevations just below 2,000 ft. Cory states:

It seems probable that *Styrax youngae* is a species of northern Mexico, for at this point in far western Texas there are mountains on both sides of the Rio Grande. Inasmuch as the plant has not been found in the 29 intervening years since its original collection, this species must be rare and at its northern limit in the Davis Mountains of southwestern Texas. It is known that *Styrax* has disappeared from localities where once it was not uncommon, and it seems true that at the present time, it grows in places inaccessible to the Angora goat, or in places where this animal is not grazed. The circumstantial evidence is that the foliage of *Styrax* is palatable as a browse to these hardy animals that produce our mohair.

Three other collections of *S. youngae* are hereby recorded. Two collected in 1936 in Coahuila, Mexico (Wynd & Mueller 340, GH, MO, NY) were, if seen by Cory, not detected as being *S. youngae*. The other collection was made in 1960 in Nuevo León, Mexico (Smith M149, TEX). These collections confirm Cory's suspicions that *S. youngae* is indeed a species of northern Mexico. These specimens have slightly more dense pubescence on the undersurface of the leaves and on the calices and pedicels than does the holotype, but other characteristics fit the species so that identification is certain. All of these collections were made at higher elevations (4,000–4,500 ft.).

6. STYRAX OFFICINALIS Linnaeus.

Key to Varieties

Leaf blades broadly ovate to slightly orbicular, glabrous or with scattered stellate trichomes below; calices faintly pubescent; range centers in north central California (Fig. 7). 6a. *S. officinalis* var. *californica*
 Leaf blades usually suborbicular, sometimes ovate-orbicular, heavily fulvescent pubescent below; calices tomentose with general prevalence of rufous hairs; range centers in southern California (Fig. 7).

. 6b. *S. officinalis* var. *fulvescens*

6a. *STYRAX OFFICINALIS* Linnaeus var. *CALIFORNICA* (Torrey) Rehder,
 Mitt. Deutsch. Dendrol. Ges. 1915: 226. 1915.
Styrax californica Torr., Smithsonian Contrib. 6(IV): 1-8, t. 12. 1853.
Styrax officinalis L. var. *californica* (Torr.) Munz and Johnson, Bull.
 Torrey Bot. Club 51:297. 1924.

Shrub to 3 m, upright, branching, with irregular crown. Leaves glabrous to lightly pubescent below, blades broadly ovate to slightly orbicular, 4-6 cm long, margins entire, bases obtuse to rounded, apices acute to obtuse; upper surfaces light green, smooth; lower surfaces paler, often with very fine scattered stellate trichomes; veins slightly impressed; petioles 5-8 mm long, slender, glabrous or very faintly pubescent. Flowers in terminal or axillary, 3-5 flowered racemes, borne on short leafy branches; calices 5-7 mm long, faintly pubescent, shallowly toothed, teeth acute; corolla lobes 12-15 mm long, oblong to obovate, apices acute, surfaces with soft downy pubescence along the borders fading inward; stamens about 2 mm shorter than corolla lobes; filaments pubescent throughout their length; anthers 1/3 the length of the stamens; style barely exceeding the corolla lobes, pubescent on the proximal 1/2; stigma barely lobed. Drupes maturing August-September, globose, 8-10 mm in diameter, style persistent as an apiculation; seeds subglobose, shining, smooth, longitudinally grooved (Fig. 7).

Styrax officinalis var. *californica* occurs generally in the foothills of the Sierra Nevadas along watercourses from 500 to 3,500 ft. elevation (Jepson, 1963). From Siskiyou County, its northernmost locality, it ranges southwestward to Lake and Alameda counties, eastward to Eldorado and Placer counties and then to Fresno County, its southern limit (Fig. 18). Jepson (1963) gives the southernmost extension as San Bernardino County, but I have not seen material from this county that I would call var. *californica*. The known range of var. *californica* was, before my study, much more restricted than presently, extending only from Shasta County south to Amador and Calaveras counties (Copeland, 1938).

The flowers appear from April through mid-May. The colloquial name is "Snowdrop bush."

Holotype: U.S.A. CALIFORNIA. Sacramento Co.: Upper Sacramento. Fremont, 1845-47 (NY!).

UNITED STATES. CALIFORNIA. Alameda Co.—Bracelin 1235 (F, NY), Bracelin 2586 (F, NY), Berkeley, Kelee (UNC). Amador Co.—Glenco, Belshaw 2379 (UNC). Butte Co.—Enterprise, Heller 1 1891 (F, GH, MO, NY,

UNC). Calaveras Co.—Mokelumne R., *Hanson* 227 (GH, MO, NY). Colusa Co.—Clear Lake, *Hoover* 4988 (UNC); Leesville, *Heller* 13111 (F, GH, MO, NY, PH); Bear Valley, *Bacigalupi* 3187 (NY, UNC). El Dorado Co.—*Natoma* Ditch, *Brandegee*, 14 May 1907 (PH); American River, *Smith* 2540 (UNC). Fresno Co.—Mill Creek, *Bacigalupi* 7686 (FSU). Glenn Co.—Neesville, *Heller* 11535 (F, GH, MO, NY, PH, UNC). Lake Co.—Leesville, *Abrams* 12577 (NY); Sulphur Banks, *Eastwood* 5640 (F, GH); Williams, *Clausen* 1027 (UNC); Clear Lake, *Carter* 353 (UNC); Borax Lake, *Simontacchi* 264 (UNC); Soda Bay, *Neuns* 165 (UNC), *Schulthers*, 9 Aug 1931 (UNC), *Hastings*, 28 Apr 1940 (UNC), *Howell* 15589 (GH); Bartlett Springs, *Bleedlove* 5180 (DUKE, SMU); Servier Lake, *Bowmann*, 11 May 1901 (GH). Placer Co.—Auburn, *Carter* 1485 (GH, NY, UNC); Auburn, *Crum* 2043 (UNC); Colfax, *Hitchcock* 6391 (NY); Forest Hill, *Jump*, 15 May 1939 (GH, UNC). Sacramento Co.—Upper Sacramento, *Pringle* 14757 (F, GH, MO); Sacramento R., *Capt. Wilkes*, 1838 (NY), *Fremont*, 1845 (NY), *Hulse* (NY); Folsom, *Copeland* 1614 (GH, UNC), *Nordstron* 79 (UNC). Shasta Co.—Redding, *Johannsen* 149 (NY), *Johannsen* 122 (UNC), *Hitchcock* 6486 (MO, UNC), *McVaugh* 6238 (UNC), *Grant* 7976 (UNC), *Balls* 20724 (NY); Kennett, *Eastwood* 1455 (GH), *Smith* 168 (GH); Lemoine, *Eastwood* 1804 (GH), *Rose* 34238 (F, NY, SMU); Pitt R., *Mason* 5876 (GH, UNC), *Heller* 13498 (F, MO, NY), *Jones*, 16 Jul 1931 (MO), *Brown* 273 (F, NY, UNC); Delta, *Jepson* 6177 (NY); Whiskey Town, *Howell* 29185 (NY), *Rose* 54029 (NY); Trinity, *Balls* 18665 (NY); Tall House, *Baker*, 30 Apr 1900 (UNC); Weaverville, *Josephson* 24 (UNC); Baird, *Coombs*, 9 Jul 1915 (GH). Siskiyou Co.—Pitt R., *McMinn* 2493 (UNC); McCloud, *Sculphan* 150 (NY). Tehama Co.—Paskenta, *Crampton* 7773 (UNC). Yuba Co.—Strawberry Valley, *Burks* 38 (UNC); Smartville, *Josephson* 37 (UNC).

The type locality, "Upper Sacramento," means the neighborhood of the Sacramento and the Pitt rivers in what is now Shasta County.

The nomenclature of this taxon is rather confusing. Its present rank is due to its strong resemblance to *S. officinalis* of southern Europe, from which it is chiefly distinguished by its few-flowered racemes, thickened pedicels (a character that does not hold up), and longer staminal tube. After Torrey (1853) described *S. californica*, it was reduced by Perkins (1907) to synonymy under *S. officinalis* and then resurrected by Rehder (1915) and, independently, by Munz and Johnston (1924) as *S. officinalis* var. *californica*. So the distribution of *S. officinalis* is the Mediterranean region and California. The movement of this entity through the land bridges that occurred across the Bering Sea is quite possible, as many species of animals and plants are known to have accomplished this. Several species of *Styrax* are represented in Asia. Some of them resemble *S. officinalis*. Among these are *S. macranthus* Perk. of central Asia, *S. japonicus* Sieb. and Zucc. of Japan, *S. obassia* Sieb. and Zucc. of China and Japan, and *S. odoratissimus* Champ. of China. The last species occupies the northernmost range of those mentioned. Perhaps elements of *S. officinalis* moved northwestward during interglacial periods, eventually crossing the Bering Sea land bridge. As the climate cooled

once again, the glaciers returned, destroying the species over much of the former range by forcing it south into terrain not suitable for it. Little is known of the fossil record of *Styrax*, especially in the region concerned.

The California material differs from the Mediterranean material in the characters mentioned and in pubescence, being glabrate or lightly tomentose on the underside of the leaves instead of closely white tomentose. This pubescence is dimorphic along the veins and midrib, with dark colored trichomes being scattered among and projecting above the pallid mass of the tomentum. Also, the style in Mediterranean material appears to be less compressed than in California material and is evidently less lobed (Munz and Johnson, 1924).

In that only differences between the European and the Californian examples are minor, being neither constant nor significant, I agree with Munz and Johnston (1924) and Copeland (1938) and treat the Californian material as varieties of *S. officinalis*.

For information concerning the embryology of *S. officinalis* var. *californica* the reader is referred to Copeland (1938).

6b. *STYRAX OFFICINALIS* Linnaeus var. *FULVESCENS* (Eastwood) Munz and Johnston, Bull. Torrey Bot. Club 51: 295-302. 1924.

Styrax californica Torr. var. *fulvescens* Eastw., Bot. Gaz. 41: 283-296. 1906.

Leaf blades broadly ovate-orbicular to subcordate, 4-6 cm long, margins entire, bases broadly ovate to subcordate, apices obtuse or abruptly acuminate, only slightly longer than broad; upper surfaces light green, smooth to roughened, glabrous or with a few scattered stellate trichomes; lower surfaces much paler, pubescent to densely tomentose. Calices 5-7 mm long, shallowly toothed, teeth acute, usually white tomentose (Fig. 7).

According to Munz and Johnston (1924), var. *fulvescens* ranges along the coastal slopes of California from the mountains near Santa Barbara to those near San Diego. The ranges of the two varieties (var. *californica* and var. *fulvescens*) are widely separated, with Santa Barbara County the northernmost extension. The known range of var. *fulvescens* is here extended as far north as Mendocino and Butte counties (Fig. 18).

The flowers appear from mid-April through May. The colloquial name is "Hairy snowdrop bush."

Holotype: U.S.A. CALIFORNIA. Santa Barbara Co.: Painted Cave Ranch, Santa Barbara Mountains. Wolf, 17 May 1904 (GH!).

UNITED STATES. CALIFORNIA. Amador Co.—Zion, Hansen 840 (UNC). Butte Co.—Bidwell, May 1879 (GH). Calaveras Co.—Mokelumne Hill, Blaisdell (GH); Golden Gate Hill, Rosemary 225 (UNC); Calaveras R., Stanford 300 (GH, MO). El Dorado Co.—Salmon Falls, Robbins 1934 (GH, UNC). Fresno Co.—Trimmer, Bucksloe, 10 May 1953 (GH, UNC); Trimmer, Clark 46-14 (GH), Quibell 1927 (NY, UNC), Quibell 1565 (DUKE); Kings R., Crawford 25n (UNC). Lake Co.—Mt. Konocti, Blankinship, 1 May 1924 (MO); Lower Lake, Cuff 133 (UNC); Hough Springs, Abrams 6273 (NY, US). Meno-

docino Co.—*Vasey*, 1870 (GH). Orange Co.—Star Canyon, *Hutt* 373 (DUKE); Trabuco Canyon, *Smith* 5453 (F); Corona, *Lewis* 380 (UNC). Placer Co.—Folsom, *Wolf* 8609 (GH, MO, NY). Riverside Co.—Temecula, *Stubblefield*, 2 May 1938 (NY); Elsinore, *Spring* 34 (UNC). Sacramento Co.—Folsom, *Copeland*, 30 Apr 1939 (GH, F, MO, NY, UNC). San Bernardino Co.—Cajou Pass, *Craig* 922 (GH); San Bernardino Mts., *Parish*, 29 May 1888 (UNC), *Parish*, Apr 1887 (MO), *Parish* 307 (GH, MO, NY, PH, UNC), *Parish* 11389 (UNC); San Bernardino, *Lemmon*, May 1878 (F); Waterman Canyon, *Jepson* 551 (VDB); San Savaine, *Ewan* 10982 (GH, MO); Mts., *Engelmann* 20 Sep 1880 (GH, MO); San Bernardino Mts., *Clark* 15916 (SMU); Big Bear Lake, *McMinn* 1560 (UNC). San Diego Co.—Rainbow, *Jensen* 141 (UNC); Fall Brook, *Parry*, May 1883 (MO); Mesa Grande, *Gander* 200 (UNC), *Spencer* 1147 (NY); Luis Rey R., *Mason* 3138 (GH, UNC); Henshaw Dam area, *Munz* 10353 (GH, UNC). San Luis Co.—Nipomo, *Lee* 635 (UNC). Santa Barbara Co.—Santa Inez Mts., *Wolf* 2302 (UNC); Painted Cave Ranch, *Eastwood* 33 (F, GH, MO, NY, UNC), *Wiggins* 8508 (GH); Santa Barbara, *Brandegee*, 1888 (F); Rattlesnake Canyon, *Mason* 456 (GH, UNC).

Eastwood (1906) first described this variety as *S. californica* var. *fulvescens*: "Differs from the typical *Styrax californica* in the broader, rounder leaves, cordate at base, the much denser stellate tomentum, and the general prevalence of rufous hairs especially on the calyx." Munz and Johnston (1924) created a new combination, *S. officinalis* var. *fulvescens*, which I accept for reasons previously discussed.

This variety ranges over a much greater area than originally thought. The ranges of var. *californica* and var. *fulvescens* do overlap considerably. Within this overlap are intermediate forms with various degrees of pubescence. Thus, while the two varieties are generally separated geographically, there does exist an area, which includes El Dorado, Amador, and Calaveras counties, in which intermediates occur.

7. STYRAX JALISCANA Watson, Proc. Amer. Acad. Arts 26:144. 1891.

Styrax officinalis L. var. *jaliscana* (Wats.) Perkins, Pflanzenreich IV. 241 (Heft 30); 82. 1907.

Shrub to 1 m, rather freely branched. Leaves subsessile, blades round-ovate or oblong-ovate, 4–10 cm long, the bases obtuse or somewhat cuneate, margins entire, apices abruptly short-acuminate; upper surfaces pale, densely white tomentose and reticulately veined; petioles 3–4 mm long, densely white tomentose. Flowers in axillary, 1–5 flowered racemes, 8–12 mm long; pedicels 4–6 mm long, densely white tomentose; calices 5–7 mm long, densely white tomentose, very evidently dentate, teeth 5–7, length 1–1.7 mm, acute; corolla lobes 12–14 mm long, oblong to elliptic-ovate, apices obtuse to acute, surface with soft downy pubescence; stamens 2–3 mm shorter than corolla lobes; filaments pubescent near the bases; style barely longer than the corolla lobes, essentially glabrous and slightly lobed. Drupes 8–12 mm in diameter, depressed-globose; seeds usually 3, smooth, with a ridge running from the hilum sideward (Fig. 8).

New branchlets densely white tomentose. Teeth evident on persistent calices.

Styrax jaliscana occurs on rocky hillsides and rather dry slopes. Although only a few collections are available, they attest to the wide range of this species, which extends from northern Baja California through southern Mexico (Fig. 19).

Holotype: MEXICO. JALISCO. Near Guadalajara, Pringle 2978, 10 Nov 1889 (GH!).

MEXICO. BAJA CALIFORNIA. Sierra Laguna, Gentry 4420 (GH, UNC).

GUERRERO. Galeana, Hinton 4583 (NY).

JALISCO. Near Guadalajara, Pringle 2978 (GH), Pringle 4416 (F, MO, NY, PH, US, UNC), Pringle 11012 (F, MO, NY, US).

SINALOA. Sierra Surotato, Gentry 6244 (MO, NY).

Standley (1924) states that *S. jaliscana* may not be specifically distinct from *S. officinalis*. In gross morphology it does resemble the California varieties of the latter species, especially var. *fulvescens*, but, on closer examination, differences of specific rank may be seen. The leaves of *S. jaliscana* have a slightly larger length/width ratio and are more acuminate, whereas those of *S. officinalis* tend to be more acute to very short-acuminate. Leaf pubescence in the latter species at its densest, in var. *fulvescens*, is moderate as compared to the dense woolly pubescence of *S. jaliscana*, which persists on young branchlets and racemes. The calices of both species differ not only in pubescence but also in presence of teeth, these being much more prominent in *S. jaliscana*. These two species may well be closely related but they have diverged enough to warrant separation.

Styrax jaliscana is an extremely wide-ranging species. The collections from Sinaloa and Baja California have larger leaves, up to 10–12 cm long, than do the type and other collections from Jalisco. The species is probably relatively rare because only scattered collections are available.

There are no species currently known from its range that, on morphological grounds, could have given rise to *S. jaliscana*. Therefore, I must conclude, as Standley did, that its closest relative is *S. officinalis*.

8. STYRAX GLABRESCENS Bentham

Key to Varieties

Leaves essentially glabrous below (may have stellate trichomes in the vein axils); calices stellate pilose with rufous or yellowish hairs (Fig. 9).

..... 8a. *S. glabrescens* var. *glabrescens*

Leaves lightly to densely pilose below; calices minutely grayish tomentulose (Fig. 9). 8b. *S. glabrescens* var. *pilosus*

8a. STYRAX GLABRESCENS Bentham var. GLABRESCENS, Pl. Hartweg. 66. 1839.

Styrax guatemalensis J. D. Smith, Bot. Gaz. 15: 27, 28. 1890.

Small tree, 6–12 m high, spreading. Leaves essentially glabrous, ovate-

obovate to elliptic, the blades 8–14 cm long, 4–7 cm wide, the bases cuneately narrowed to nearly rounded, margins entire to distally toothed, apices short to long acuminate; upper surfaces dark green, glabrous; lower surfaces paler, glabrous or with a few scattered stellate trichomes; surfaces reticulate-veiny; petioles 6–10 mm long, lightly stellate pubescent. Flowers in axillary, semi-drooping, 4–12 flowered racemes, 2–8 cm long, tomentose; calices 5–6 mm long, tomentose, with rufous hairs, shallowly toothed, teeth acute; corolla lobes 12–16 mm long, ovate-elliptic, apices obtuse to acute, surfaces with soft down pubescence; stamens about 2 mm shorter than corolla lobes; filaments with scattered stellate trichomes; style essentially glabrous; stigma slightly lobed. Drupes globose to subglobose, 8–12 mm in diameter, covered with dense matted tomentum; style not persistent; seeds usually 1, pale brown, with slightly roughened texture, with 2–3 grooves running from the hilum sideward (Fig. 9).

New twig growth covered with light stellate pubescence. Racemes covered with pubescence grading into dense tomentum toward the calices.

Styrax glabrescens var. *glabrescens* occurs in mountainous regions along streams, on rocky slopes, and in heavy forest from southern Costa Rica through Honduras and Guatemala and into Mexico as far north as Hidalgo (Fig. 19).

Holotype: MEXICO. VERA CRUZ. Near Jalapa. Linden, Jun 1838 (K; photograph of holotype examined).

COSTA RICA. ALAJUELA. La Palma de San Ramon, Brenes 6734 (NY), Brenes 3986 (F, NY), Brenes 13599 (NY), Brenes 6079 (F, GH, NY), Brenes 6734 (GH).

CARTAGO. El Muneco, Standley 3350 (US), Standley 51137 (GH, US).

GUATEMALA. ALTA VERAPAZ. Carcha, Standley 70316 (F); Sasis, Smith 1690 (GH, US).

EL QUICHE. Chajul, Sharp 4684 (F), Sharp 4673 (F).

HUEHUETENANGO. Barillos, Holdridge 2338 (F), Steyermark 49738 (F).

QUEZALTENANGO. Las Nubes, Standley 8397 (F); San Martin, Standley 67865 (F).

SAN MARCOS. Tecutla, Steyermark 36807 (F); Finca, Steyermark 37378 (F).

SUCHITEPEQUEZ. El Naranjo, Steyermark 46750 (F).

HONDURAS. COMAYAGUA. Cordillera Montecillos, Molina 7233 (F, US); El Achote, Yuncker 6175 (F, GH, MO).

LA PAZ. Montana Verde, Molina 24404 (F).

MEXICO. CHIAPAS. Siltepeg, Matuda 5102 (F); Boqueron, Matuda 5410 (F, MO); Letrero, Matuda 17816 (F), Matuda 4335 (GH, MO, NY, US); Rancho Phoenix, Purpus 10612a (F); Fenes, Purpus 10088 (NY); Monserrate, Purpus 10521 (GH, UNC).

HIDALGO. Zacualtipán, Moore 3231 (UNC), Martinez, Apr 1941 (GH); Honey Station, Pringle, 17 Jun 1908 (US); Trinidad, Pringle 13104 (MO, F, US).

OAXACA. Montebello, Reko 4136 (US); Cuyamecalco, Conzatti 3480 (US); La Sole de Vega, Carlson 2710 (F).

PUEBLA. Huauchinango, Lundell 12631 (UNC, US); Villa Juarez, Rzedowski 17211b (TEX).

VERACRUZ. Jalapa, Pringle 8129 (F, GH, MO, NY, UNC, US), McDaniels 942 (F); Huatusco, Purpus 1920 (UNC); Jalapa, Galeotti 2851 (US).

Wood and Channell (1960) mention that *S. glabrescens* is a close relative of *S. grandifolia*. The latter species is a tetraploid, but no chromosome counts of the former have been made so no relationship along these lines can be established. They do, however, resemble each other in many morphological features. The leaves of both have the same texture, but those of *S. glabrescens* lack the dense matted pubescence characteristic of *S. grandifolia*. Leaf shape differs somewhat, being broadly elliptic in the former and obovate in the latter species. The flowers are slightly larger in *S. glabrescens* and the petals have a slight purple tint contrasting to the creamy white petals of *S. grandifolia*. A good case for their close relationship exists but cytological work would be necessary for proof.

Standley (1938) says of *S. glabrescens*, "Frequent in forest of the Pacific slope, mostly at elevations of 500-1,500 meters; region south of Cartago; region of San Ramon. Extending to Mexico. Easily recognized among Costa Rican species because of the broad, thin, almost glabrous leaves, green on the lower surface."

Styrax guatemalensis, described by Smith (1890), is treated here as a synonym of *S. glabrescens*. Smith states that it differs from the latter species by its ovate leaves, its one-half larger flowers, and its ovate petals. However, the leaves and flowers are identical to those of *S. glabrescens*.

8b. *STYRAX GLABRESCENS* Bentham var. *PILOSUS* Perkins, Pflanzenreich IV. 241 (Heft 30): 72. 1907.

Styrax pilosus (Perkins) Standl. Contr. U.S. Natl. Herb. 23:1129. 1924.

Leaves ovate to obovate-elliptic, blades 6-12 cm long, 3-6 cm broad; upper surfaces dark green, essentially glabrous; lower surfaces pale green, light to densely pilose; petioles 6-10 mm long, tomentose-pilose. Calices 4-5 mm long, stellate pilose with rufous hairs (Fig. 9).

New twig growth and racemes are stellate-pilose with rufous hairs.

Styrax glabrescens var. *pilosus* has a much more restricted range than var. *glabrescens*. It occurs in mountainous regions along streams, on rocky slopes, and in heavy forest in Chiapas, Oaxaca, Veracruz, and Hidalgo (Fig. 19).

Holotype: MEXICO. OAXACA. Chinantla and Rincon. Galeotti 2852, May 1844 (NY!).

MEXICO. CHIAPAS. Escuintla, Matuda 15995 (F), Matuda 4179 (GH, MO, NY, US); LaConcordia, Matuda 15922 (F); Monserrate, Purpus 9280 (UNC, US); Fenix, Purpus 10545 (GH, UNC); Jitotol, Breedlove 10188 (NY).

HIDALGO. Zacualtipán, Martinez, May 1940 (GH).

OAXACA. Galeotti 2852 (NY, US); Chinantla, Galeotti 3852 (F).

VERACRUZ. Chiconquiaco, Pompa 793 (GH).

Only a few collections of this variety have been made since it was described by Perkins (1907). Standley (1924) raised this variety to specific rank. Since the only differences between the species and its variety are relatively minor ones I am herein following Perkins' designation of this taxon as var. *pilosus*.

9. *STYRAX ARGENTEUS* Presl

Key to Varieties

Leaves covered beneath with a minute, very close, stellate tomentum (Fig. 11c). 9a. *S. argenteus* var. *ramirezii*
Leaves covered below with coarse spreading stellate hairs, the pubescence velutinous.

Leaves less than half as wide as long; racemes and new branchlets covered with very short stellate pubescence beset with lepidote trichomes (Figs. 10 & 11). 9b. *S. argenteus* var. *argenteus*

Leaves half or more as wide as long; racemes and new branchlets covered with coarse, long, spreading velutinous pubescence. (Figs. 10 & 11). 9c. *S. argenteus* var. *hintonii*

9a. *STYRAX ARGENTEUS* Presl var. *ARGENTEUS*, Rel. Haenk. II. 60. 1836.

Strigilia argentea Miers, Contrib. Bot. I:185. 1851-1861.

Styrax punctatum Smith, Enum. Pl. Guatimal. 4:104. 1895.

Styrax myristicifolius Perkins, Bot. Jahrb. Syst. 31:481. 1902.

Small tree, 6-11 m high, rather freely branched. Leaf blades oblong-elliptic, 7-14 cm long, 2.5-4.5 cm broad, margins entire, the bases cuneate to rounded or obtuse, apices short acuminate; upper surfaces glabrous, darker green, smooth to slightly coriaceous; lower surfaces paler, covered with medium length, semi-spreading stellate trichomes, the pubescence slightly velutinous, petioles 2-2.5 cm long. Flowers in axillary or terminal, semi-drooping, 6-12 flowered racemes, 6-9 cm long; pedicels 6-8 mm long, short velutinous stellate pubescent, with minute bracts basally and midway its length; calices 4-5 mm long, minutely toothed, covered with short stellate pubescence mixed with lepidote trichomes; corolla lobes 8-10 mm long, oblong-linear, acute, covered outwardly with very short, fine, soft pubescence; stamens barely shorter than corolla lobes; filaments with spreading stellate trichomes, with tufts of long trichomes basally; anthers about $\frac{1}{2}$ the length of the stamens; style glabrous, about as long as stamens; stigma slightly lobed. Drupes 10-13 mm in length, 6-8 mm in diameter, oblong-elliptic, lepidote trichomiferous; seeds 1, 10-11 mm long, glossy brown, with a ridge running from the hilum sideward (Figs. 10 & 11).

New branchlets, racemes, and petioles slightly velutinous, covered with soft, short hairs.

Styrax argenteus var. *argenteus* occurs along wooded slopes throughout much of western Mexico and Central America. It extends from Sinaloa,

Mexico to Coclé, Panama, being especially prevalent in southern Mexico and Guatemala (Fig. 20).

Holotype: MEXICO. Haenke 148 (MO!).

COSTA RICA. ALAJUELA. Zarcero, Smith, 12 Aug 1937 (F).

GUANACASTE. Liberia, Williams 25087 (F); La Cruz, Jimenez 345 (F).

HEREDIA. Heredia, Williams 16067 (F, GH).

SAN JOSE. Finca Tablera, Jimenez 3511 (NY).

EL SALVADOR. CHALATENANGO. La Palma, Allen 7314 (F).

SANTA ANA. Cerro Verde, Allen 6853 (F, US).

GUATEMALA. ALTA VERAPAZ. Tactic, Standley 92631 (F).

BAJA VERAPAZ. El Ranchio, Kellerman 7642 (F, NY, US).

CHIMALTENANGO. San Martin, Standley 57958 (F); Morales R., Martin 1208 (F).

CHIQUIMULA. La Laguna, Steyermark 30728 (F); San Jose, Steyermark 31150 (F).

EL PROGRESO. Finca Piamonte, Steyermark 43593 (F).

EL QUICHE. Aguilar 1395 (F).

GUATEMALA. Barrauea, Smith 2266 (F, GH, US); Sanarate, Kellerman 6415 (F).

HUEHUETENANGO. San Juan, Standley 83018 (F); San Sebastian, Steyermark 50429 (F), Standley 82830 (F, MO, US); San Juan, Standley 81378 (F); Aguacatan, Skutch 1935 (F, GH, NY, US); Carrizal, Steyermark 50776 (F, US); Libertad, Steyermark 51100 (F); Selegua, Molina 21341 (F, NY).

JALAPA. El Rancho, Kellerman 5664 (US); Jumay, Steyermark 32340 (F, US); Monjas, Standley 77656 (F).

ZACAPA. Rio Sitio Nuevo, Steyermark 43199 (F); Reforma, Steyermark 42075 (F, NY).

HONDURAS. CHOLUTECA. San Marcos, Standley 15947 (F), Standley 15875 (F).

COMAYAGUA. Comayagua, Standley 5686 (F); Siquatipeque, Standley 6344 (F), Yuncker 5589 (F, GH, MO, US); San Antonio, Williams 12314 (F, US).

MORAZAN. Jicarito, Williams 14028 (F, GH); Chaquite, Williams 12136 (GH, F, MO); Rio Capa Rosa, Williams 12707 (F, GH); Zamorano, Rodriguez 3669 (F, UNC), Standley 1674 (F), Molina 20321 (F, NY); Chahite, Standley 5007 (F).

MEXICO. CHIAPAS. Tenejapa, Breedlove 6366 (F, FSU), 7619 (F), 6439 (F); Jitotol, Breedlove 8917 (F); Trinitaria, Breedlove 14085 (F); Pass de Cura, Bosse 8222 (F); Ocosingo, Shilom 3431 (F); Escuintla, Matuda 16256 (MO); Monserrate, Purpus 46 (US); Rancho Fenin, Purpus 14301 (GH); San Vincente, C. Goldman 872 (US).

GUERRERO. Carnotla, Rzedowski 18529 (TEX).

JALISCO. San Sebastian, Mexia 1351 (F, GH, MO, NY, UNC, US), Mexia 1861 (UNC, US).

MICHOACAN. Coahuayula, Emrick 60 (F); Morelia, Arsene 2841 (US).

OAXACA. Santa Ana, Conzatti 4558 (NY, US); Concordia, Rexo 3642 (US).

SINALOA. Suratato, Standley 5164 (GH, NY, UNC); San Juan, Ortega 4118 (US); San Ignacio, Montes 714 (US); Cerro Colardo, Henry 5164 (F, MO).

MEXICO. Villareda, Hinton 7410 (GH, MO, US); Luvianos, Hinton 5309 (F, GH), Hinton 6193 (NY, US).

NICARAGUA. MATAGALPA. Jinotega, Williams 23955 (F, NY, US); Sebaco, Webster 12496 (F, GH).

PANAMA. CHIRQUI. Boquete, Stern 2045 (MO); El Volcán, Tyron 826 (FSU).

COCLE. Ola, Pittier 5076 (GH, NY, US).

The nomenclature of *S. argenteus* has been greatly confused since Presl (1836) first described this taxon. Eleven species since described I place in synonymy with *S. argenteus*. *Styrax hintonii* and *S. ramirezii* are treated as varieties of *S. argenteus* because they represent the extremes of variation exhibited by this species.

When Greenman (1899) described *S. ramirezii*, he evidently did not realize the entire array of variation in the *argenteus* complex. Therefore, it was reasonable for him to assume he had a new species. From 1902–1906 Perkins described seven new species. She was a definite “splitter,” for although she examined a fairly wide array of material, she insisted on segregating new taxa on mostly minor and inconsistent characters. I have examined the type specimens of the seven species; the reduction of these species to synonymy is justified.

Standley (1924) recognized *S. ramirezii*, *S. cyathocalyx* Perkins, and *S. polyneurus* Perkins. However, on specimens in the U.S. National Herbarium, I noticed that his annotations since 1924 indicate he later considered them all *S. argenteus*. The characters he used to separate these three taxa from *S. argenteus* are those that Perkins later used, namely, pubescence on the lower side of the leaf, flower length, and calyx length. These characters are very inconsistent and were used by Perkins to separate the five other new taxa she described from the *argenteus* complex. In short, Perkins took the variations found in the complex and described new species with total disregard for the continuum of variation.

In this treatment I have placed in synonymy with *S. argenteus* most of the species that Perkins segregated from the *argenteus* complex. A cytological study is in order for this complex and until such is done the relationships among the taxa will not be established definitely.

The following chart indicates the differences between the species and its varieties:

var. <i>argenteus</i>	var. <i>hintonii</i>	var. <i>ramirezii</i>
Leaves less than half as broad as long; covered below with short spreading stellate trichomes.	Leaves half or more as broad as long; covered below with coarse, long, velutinous pubescence.	Leaves less than half as broad as long; covered below with dense, fine, matted, tomentum.

Racemes and new branchlets covered with short spreading stellate trichomes beset with lepidote scales.

Racemes and new branchlets covered with coarse, long, spreading velutinous pubescence.

Racemes and new branchlets covered with dense, fine, matted tomentum beset with lepidote scales.

9b. *STYRAX ARGENTEUS* Presl var. *hintonii* (Bullock) Gonsoulin, comb. nov.

Styrax hintonii Bullock, Kew Bull. 1936. :366-368. 1936.

Styrax magnus Lundell, Bull. Torrey Bot. Club 66:600. 1939.

Styrax vulcanicola Standl. and Steyermark, Field Mus. Publ. Bot. 22:264. 1940.

Small tree, 3–10 m high, the crown spreading. Leaf blades oblong-elliptic, 9–12 cm long, 4–7 cm wide (with extremes up to 20 cm long and 10–11 cm wide), margins entire, the bases rounded or obtuse, apices short acuminate to rounded; upper surfaces glabrous, dark green, smooth to coriaceous; lower surfaces covered with coarse, long spreading stellate trichomes, the pubescence distinctly velutinous; petioles 2–2.5 cm long, covered with coarse, long, spreading velutinous pubescence. Flowers in 6–10 flowered racemes, 2.5–4 cm long; pedicels 6–10 mm long, covered with long, spreading, velutinous pubescence; calices 5–6 mm long, minutely toothed, teeth acute, covered with long, spreading, velutinous pubescence; corolla lobes 9–11 mm long, oblong-linear, apices acute, covered outwardly with coarse matted stellate pubescence (Figs. 10 & 11).

Styrax argenteus var. *hintonii* occurs occasionally in dry mountainous regions but more often on damp wooded slopes of lower elevations. It ranges in the western regions of Mexico from Jalisco south to and throughout Guatemala (Fig. 20).

Holotype: MEXICO. MICHOACAN. Calera 770 m, wet barranca. Hinton 3798, 19 Apr 1933 (MO! isotypes: F! GH! US!).

GUATEMALA. GUATEMALA. San Raimundo, Standley 62879 (F, NY).

HUEHUETENANGO. Cuilo, Steyermark 50699 (F, US).

SAN MARCOS. San Fafael, Standley 68618 (F); Tecutla, Steyermark 36801 (F); San Rafael, Steyermark 36234 (F).

QUEZALTENANGO. San Martin, Standley 85557 (F).

MEXICO. CHIAPAS. Ghiesbreght 62081 (GH, MO).

GUERRERO. Yesceros, Hinton 14404 (GH), Hinton 14409 (US).

JALISCO. Autlan, McVaugh 10304 (NY, TEX); San Sebastian, Mexia 1504 (F, GH, MO, NY, US, UNC).

MICHOACAN. Morelia, Arsene 5366 (GH, MO, US), Arsene 8472 (MO, US), Arsene 2841 (GH, MO, NY); Zitacuaro, Rzedowski 18371 (TEX); Calera, Hinton 3798 (F, GH, MO, US), Hinton 7605 (F, GH, MO, PH, TEX, US); Nanchititla, Hinton 7618 (GH, MO).

Styrax argenteus var. *hintonii* represents one end of the spectrum of variation in the *argenteus* complex. The pubescence of var. *hintonii* is velutinous,

being of very long, spreading, stellate hairs. The pubescence of var. *argenteus* is shorter. The leaf length/width ratio is greater in var. *argenteus* than in var. *hintonii*. Leaf size varies greatly as can be seen in *S. magnus* Lundell, which represents a large leaf form of var. *hintonii*. *Styrax vulcanicola* Standl. and Steyermark represents an intermediate between var. *argenteus* and var. *hintonii* but with characters closer to the latter.

9c. *STYRAX ARGENTEUS* Presl var. *ramirezii* (Greenman) Gonsoulin, comb. nov.

Styrax ramirezii Greenm. Proc. Amer. Acad. Arts 34: 569. 1899.

Styrax micranthus Perkins, Bot. Jahrb. 31: 480. 1902.

Styrax polyanthus Perkins, Bot. Jahrb. 31: 479. 1902.

Styrax warscewiczii Perkins, Bot. Jahrb. 31: 480. 1902.

Styrax polyneurus Perkins, Bot. Gaz. 35:5. 1904.

Styrax cyathocalyx Perkins, Repert. Spec. Nov. Regni Veg. 2 (14/15): 24. 1906.

Styrax orizabensis Perkins, Repert. Spec. Nov. Regni Veg. 2(14/15): 25. 1906.

Small tree, 9–13 m high, the crown spreading. Lower surfaces of leaves paler, covered with very close minute stellate tomentum; petioles 1.5–2 cm long, covered with fine stellate tomentum mixed with scattered lepidote trichomes. Flowers in 6–12 flowered racemes, 5–7 cm long; pedicels 6–8 mm long, covered with short stellate pubescence mixed with lepidote trichomes; corolla lobes 8–10 mm long, oblong-linear, apices acute, covered outwardly with matted stellate trichomes (Figs. 10 & 11).

Styrax argenteus var. *ramirezii* occurs on rather dry wooded slopes in mountainous regions of western Mexico and Central America. It extends from Michoacán, Mexico, southward throughout Central America as far as Colón, Panama (Fig. 20).

Holotype: MEXICO. MORELOS. Mountain canyons above Cuernavaca. Pringle 6848, 15 May 1898 (NY! isotypes: F! GH! MO! PH! US!).

COLOMBIA. CHOCO. Juarin, Duke 11500 (MO).

COSTA RICA. ALAJUELA. Zarcero, Smith 2700 (F). Smith 4232 (UNC), Smith 113 (NY), Smith 176 (F), Smith 1971 (GH, UNC); Palmira, Smith 2623 (F, MO), Smith 4165 (F, UNC); San Miguel, Brenes 6410 (NY); San Ramon, Brenes 3772 (NY), Brenes 3683 (NY), Brenes 17008 (NY), Brenes 3971 (NY), Brenes 6464 (NY), Brenes 5403 (NY).

CARTAGO. Vueltas, Williams 16260 (F), Williams 16131 (F); Trinidad, Wilbur 8821 (DUKE); Cartago, Chrysler 5590 (F); Guarco, Madriz 9 (F, NY).

HEREDIA. Volcan Barba, Hathaway 1258 (GH, DUKE); Barba, Lems 5340 (F, NY).

SAN JOSE. San Francisco, Smith 7079 (F, GH, NY, US); Rio Tores, Smith 7447 (GH, US); Santa Maria, Standley 42216 (US); Escasia, Standley 32549 (US); Aserri, Standley 41410 (GH, US); Rio Virilla, Tondine 17924 (F); Valerio 1378 (F); San Jose, Little 6043 (F).

EL SALVADOR. AHUACHAPAN. Guaymango, Calderon 1988 (GH, NY,

US); Finca Colima, *Standley* 20147 (GH, NY, US).

CHALATENANGO. La Palma, *Allen* 7314 (NY).

SANTA ANA. Santa Ana, *Carlson* 690 (UNC, F), *Standley* 20405 (GH, NY, US), *Allen* 6882 (F), *Williams* 13581 (GH, F).

GUATEMALA. ALTA VERAPAZ. Tactic, *Standley*, 92400 (F), *Standley* 91577 (F, NY), *Standley* 92302 (F), *Standley* 92574 (F), *Steyermark* 43937 (F), *Molina* 12236 (F, NY).

BAJA VERAPAZ. Chilasco, *Lamb* 115 (F).

CHIMALTENANGO. Volcán de Pacaya, *Conduk* 479 (MO, US).

CHIQUIMULA. Chiquimula, *Steyermark* 30624 (F).

EL QUICHE. Chazul, *Sharp* 4677 (F); Nebaj, *Contreras* 5102 (F, US), *Aguilar* 758 (F).

EL PROGRESO. Finca Piamonte, *Steyermark* 43410 (F, UNC).

ESCUINTLA. Las Lajas, *Standley* 64767 (F, GH).

GUATEMALA. San Francisco, *Standley* 80605 (F), *Standley* 80536 (F), *Standley* 80684 (F), *Standley* 80659 (F); Las Calderas, *Standley* 58420 (F, GH); La Aurora, *Aguilar* 186 (F), *Aguilar* 456 (F), *Finca Belen*, *White* 5260 (F).

HUEHUETENANGO. Barillas, *Steyermark* 48488 (F); Huitz, *Steyermark* 48666 (F); Soloma, *Steyermark* 48441 (F, GH).

JALAPA. Buena Vista, *Steyermark* 32827 (F, GH).

QUEZALTENANGO. San Geronimo, *Steyermark* 33315 (F); Santa Maria, *Steyermark* 33926 (F).

SACATEPEQUEZ. Antigua, *Standley* 63786 (F), *Standley* 63714 (F, GH, NY).

SAN MARCOS. Toma, *Steyermark* 37989 (F), *Steyermark* 36712 (F).

SANTA ROSA. Chiquimulilla, *Steyermark* 33138 (F, GH); Las Vinas, *Heyde* 6182 (F, GH, MO, NY, US).

SOLOLA. Finca Moca, *Steyermark* 47924 (F), *Steyermark* 47497 (F, GH).

SUCHITEPEQUEZ. Santa Clara, *Steyermark* 46759 (F, GH); Las Nubes, *Steyermark* 35418 (F).

HONDURAS. COMAYAGUA. San Luis, *Edwards P-290* (F, GH).

INTIBUCA. Yashee, *Molina* 6522 (US).

LA PAZ. Marcala, *Molina* 6460 (F, US).

MORAZAN. Yeguare, *Williams* 11279 (F, GH, MO, US); Tamara, *Molina* 24561 (F); *Molina* 7524 (F); Cerro Uyuca, *Standley* 8019 (F); Zamarano, *Rodriguez* 2100 (F), *Rodriguez* 3760 (F, GH, US), *Standley* 1739 (F, UNC), *Williams* 12648 (F, GH); Cuesta Grande, *Williams* 13270 (F, GH, MO, UNC); Juancito, *Williams* 17455 (F, GH).

EL PARAISO. Yuscaran, *Molina* 627 (F); Arenar, *Williams* 10491 (F, MO, PH); Danli, *Rodriguez* 2004 (F).

DISTRITO CENTRAL. *Hagen* 1253 (NY).

MEXICO. CHIAPAS. Mt. Pasitor, *Matuda* 0467 (US); Mt. Orlando, *Matuda* 0568 (US), *Matuda* 16265 (MO), *Matuda* 3930 (GH, MO, NY), *Matuda* 2668 (GH, F, NY, UNC); Capilla Bosse 8335 (F); Carmelo, *Juzepczuk* 1598 (F);

Fenix, *Purpus* 10082 (NY); Boquerron, *Purpus* 7422 (GH, NY); Mouserrate, *Purpus* 10555 (MO, NY, UNC), 10531 (GH); Fenix, *Purpus* 10157 (UNC).

GUERRERO. Ancha, *Hinton* 14750 (F, GH, MO, NY, US); Aguazarca, *Hinton* 10400 (F, GH, MO, US); Galeana, G. *Hinton* 14742 (F); Mina, *Mexia* 9059 (F, GH, MO, NY, US).

MICHOACAN. Zitauara, *Mayer* 267 (US); Tancitaro, *Nelson* 6886 (GH, US); San Filipe, *Hinton* 11831 (F, GH, MO, NY, PH, US); Morelia, *Rzedowski* 18362 (TEX).

MORELOS. Tepoxtlan, *Pringle* 9000 (F, GH, MO, US), *Pringle* 8023 (F, GH, MO, NY, PH, US); Cuernavaca, *Hitchcock* 7105 (GH, UNC, US); El Pargue, *Martinez*, Feb 1942 (UNC), *Rzedowski* 19771 (TEX); Zempoala, *Mendoza*, 14 Jun 1964 (TEX); Rose 7236 (GH, US) Chilacuate, *Martinez*, Feb 1942 (UNC); Cuernauca, *Pringle* 6848 (F, GH, MO, NY, PH, US).

OAXACA. Oaxaca, *Liebmann* 596b (F); Cnicatlan, *Conzatti* 2338 (F); La Loma, *Conzatti* 3564 (US), 2450 (F), Cuyamacalco, *Smith* 347 (GH); *Galeotto* 1687 (NY, US).

NICARAGUA. MATAGALPA. La Fundadora, *Williams* 24844 (F).

PANAMA. CHIRQUI. Viejo Valley, *White* 70 (F, GH); Camiseta, *Terry* 1338 (F, GH); Boquete, *Davidson* 776 (F, GH, US); Seco, *Woodson* 484 (F, GH); Chiriqui, *Terry* 1348 (F); Casita Alta, *Woodson* 919 (F, NY); Bambita, *Allen* 4851 (F, GH, NY, UNC); Gloria, *Pittier* 4242 (NY, US).

Styrax argenteus var. *ramirezii* represents another end of the spectrum of variation in the *argenteus* complex. It is readily separated from var. *hintonii*, which has spreading velutinous pubescence, by its possession of close matted stellate pubescence on the lower surface of the leaf. The pubescence on the lower leaf surface of var. *argenteus*, while being shorter than var. *hintonii*, still has a spreading character and is easily separated from the matted tomentum of var. *ramirezii*. Most of the intermediates interpreted by Perkins (1907) to be new species are morphologically closer to var. *ramirezii*. This is reflected in the number of species placed in synonymy with this variety.

10. STYRAX CONTERMINUS Smith, Bot. Gaz. 18:5. 1893.

Small tree, to 14 m high, with open, freely branched crown. Leaves elliptic to oblong, blades 7–14 cm long, 3–4.5 cm broad, margins entire, the bases cuneately narrowed or nearly rounded, apices counterminously acuminate; upper surfaces glabrous, coriaceous, finely reticulate veined, light green; lower surfaces pale, nowhere reticulately veined, stellate scales lacerate, lepidote, silvery sprinkled with red; petioles ferruginous, 1.2–2 cm long. Flowers in axillary and terminal, 4–8 flowered racemes, 5–8 cm long; pedicels 10–14 mm long, ferruginous, minutely bracteolate at the base and the middle; calices 4–5 mm long, minutely toothed, silvery lepidote; corolla lobes 8–10 mm long, oblong to elliptic, silvery lepidote, apices acute; stamens barely shorter than the corolla lobes; filaments half-connate, twice as long as the oblong anthers, which are mixed with fimbriate scales; style slightly longer than stamens; stigma barely lobed. Drupes slightly asymet-

rical, oblong-elliptic, 12–15 mm long, 7–8 mm wide, silvery lepidote, style not persistent; seeds usually 1, oblong-elliptic, pale brown, lustrous, with several slight longitudinal grooves running from the hilum sideward (Fig. 12).

New branchlets and racemes covered with lacerate, ferruginous, lepidote scales.

Styrax conterminus occurs along wooded slopes in mountainous regions from Santa Ana, El Salvador, through Guatemala in Huehuetenango, Quiché, and Zacapa, and into Chiapas, Mexico (Fig. 19).

Holotype: GUATEMALA. QUICHE. San Miguel Uspantan, alt. 6,000 feet. Smith 2915, Apr 1892 (MO! isotypes: GH! US!).

EL SALVADOR. SANTA ANA. Monte Cristo, Allen 7184 (F, GH, NY, US).

GUATEMALA. HUEHUETENANGO. San Juan, Steyermark 49982 (F, GH, US); Puente, Sharp 45104 (F).

QUICHE. San Miguel, Smith 2915 (GH, MO, US).

ZACAPA. Volcan Gemelos, Steyermark 43297 (F, GH, NY).

MEXICO. CHIAPAS. Naquivil, Matuda 15507 (F); Boqueron, Purpus 7422 (UNC).

In original description of *S. conterminus*, Smith (1893) states that there are three more species of the lepidote group [other than the four included in my study] but these three all are from South America. Of the four species of *Styrax* of the lepidote group included in my study, *S. conterminus* is the only one in Central America and Mexico. The other three, *S. ochraceus*, *S. portoricensis*, and *S. glaber*, occur in the Dominican Republic, Puerto Rico, and the British West Indies, respectively.

There are no species within the geographical range of *S. conterminus* with which it could be confused. Although *S. argenteus*, which has a wide range of variation in vegetative morphology, often resembles *S. conterminus*, it is readily distinguished from it by a lack of lepidote pubescence.

11. *STYRAX OBTUSIFOLIA* Grisebach, Cat. Pl. Cuba 167. 1866.

Shrub to small tree, 3–10 m high. Leaves oblong to obovate, blades 3–4 cm long, 1.5–1.8 cm broad, margins entire, the bases cuneately narrowed, apices rounded to acute; upper surfaces dark green, smooth, glossy; lower surfaces paler, covered with light, fine tomentum, with scattered lepidote trichomes. Flowers in axillary, semi-drooping, 2–6 flowered racemes, 13–15 mm long; pedicels 3–4 mm long, subtended basally by minute bracts; calices 2–3 mm long, teeth inconspicuous; racemes, calices, and pedicels covered with lepidote pubescence; corolla lobes 5–6 mm long, 1–1.5 mm wide, finely stellate pilose, apices acute; stamens barely shorter than the corolla lobes; filaments nearly glabrous; anthers $\frac{1}{2}$ the length of the stamens, glabrous; styles short, barely surpassing calyx; stigma 3-lobed. Drupes obovoid, 10–12 mm long, 4–5 mm wide, apices obtuse to acute; style basally persistent; seeds 1–2, pale brown, lustrous (Fig. 13).

Styrax obtusifolia occurs on forested slopes in mountainous regions of Cuba, in the provinces of Pinar del Rio and Las Villas, and extends into Haiti and into the western sections of the Dominican Republic (Fig. 21).

Holotype: CUBA. Wright 2931, 1860-64 (NY! isotypes: MO! UC! US!).
CUBA. LAS VILLAS. Soledad, Gonzales 477 (NY).

PINAR DEL RIO. Sierra de Rangel, Roig 4516 (NY); Rosario Mts., Bro. Alain 57 (GH), Bro. Alain 6097 (GH, US), Bro. Alain 714 (NY); La Mulata, Bro. Alain 2440 (NY); Rio Taco-Taco, Ekman 17633 (NY, US).

SANTA CLARA. Santa Clara, Britton 5451 (F, NY); Trinidad Hills, Jack 8606 (F, GH, NY, US), Jack 8089 (NY, US), Jack 7129 (F, GH, NY, US); San Juan, Howard 5618 (NY, US); Lomas de Banao, Luna 448 (NY), Luna 40 (NY).

HAITI. NORD. Bourbon, Ekman 1954 (F, NY, US).

DOMINICAN REPUBLIC. DAJABON. Partido, Liogier 16242 (NY).

Perkins (1907) indicates that *S. obtusifolia* is restricted to Cuba. However, although this is the only Cuban *Styrax*, it does extend into western Dominican Republic where its range overlaps with *S. ochraceus*. Vegetative morphology of both species is quite similar, but the flowers are strikingly different. The racemes of *S. obtusifolia* are much more lax, generally having several more flowers, in contrast to the short, rather stiff racemes of *S. ochraceus* with 2-3 flowers. The flowers of the former species, 7-9 mm long, are smaller than those of the latter, 2.5-3.4 cm long. These floral characters could not possibly be confused. The fruits of both species are similar, those of *S. obtusifolia* being 1-2 mm larger, not an appreciable difference.

12. *STYRAX OCHRACEUS* Urban, *In Symb. Ant.* 7:331. 1912.

Shrub to small tree, 3-8 m high. Leaves essentially glabrous, occasionally having scattered lepidote trichomes on the lower surfaces, blades obovate to elliptic, 2.5-5 cm long, 1.5-2.5 cm broad, margins entire, the bases cuneately narrowed, apices rounded to acute, occasionally mucronate tipped; upper surfaces dark green, smooth, glossy; lower surfaces paler, glossy; petioles 5-6 mm long, rufous stellate. Flowers in axillary, 2-3 flowered racemes, 1-1.5 cm long, subtended at the bases of the calices, midway and basally on the pedicels by minute bracts; pedicels 6-8 mm long; calyx 6-8 mm long, very shallowly toothed or teeth wanting, covered with dense rufous lepidote pubescence; corolla lobes 2-2.8 cm long, 2-3 mm wide, linear, remaining partially fused for 2/3 their length, the distant 1/3 being free and reflexed, covered with rufous stellate pubescence, lobes adnate to the calyx tube near its base; stamens 2-3 mm shorter than corolla lobes; filaments glabrous, fused basally upward for 4/5 their length and adnate to the corolla lobes for 3/4 their length; anthers 3-4 mm long; style as long as corolla lobes; stigma slightly lobed. Drupes oblong, 8-10 mm long, covered with crusty lepidote scales; seeds usually 1, pale yellowish-brown with three slight grooves running from the hilum sideward (Fig. 14).

Styrax ochraceus occurs in both mountainous cloud forest and heavily forested slopes into the high valleys. No collections have yet been made in eastern Dominican Republic, where the mountainous terrain gives way to rolling hills (Fig. 21).

Holotype: DOMINICAN REPUBLIC. LA VEGA. In Loma Rosilla. Fuertes

1766, Jul 1912 (PC; isotype: PC!).

DOMINICAN REPUBLIC. BAHORUCO. Sierra de Neiba, *Liogier* 12506 (NY), *Jimenez* 5622 (NY).

BARAHONA. Loma dela Sal, *Liogier* 11364 (NY); Jarabacoa, *Liogier* 11983 (NY).

LA VEGA. Loma Rosilla, *M. Fuertes* 1766 (NY); La Rucille, *Liogier* 12148 (NY), *Liogier* 12142 (NY); Valle Nuevo, *Ekman* 13883 (F, GH, NY, US); Constanza, *Liogier* 16105 (NY).

SAN JUAN. La Pelona, *Liogier* 12818 (NY).

Province unknown, Loma del Oro, *Liogier* 11546 (NY).

Styrax obtusifolia, which occurs mainly in Cuba, does extend into Haiti and into the northwestern section of the Dominican Republic. Here it is sympatric with *S. ochraceus*, but the two species are not easily confused. The closest relative of *S. ochraceus* seems to be *S. obtusifolia* because of its adjacent range and its strong resemblance vegetatively, but the flowers are so different as to suggest some other lineage.

Although no collections of *S. ochraceus* have been made from Haiti, much terrain there is mountainous, providing suitable habitats for its growth. No doubt it will be found in Haiti as well.

13. *STYRAX PORTORICENSIS* Krug and Urban, Bot. Jarhb. Syst. 15: 337-338. 1893.

Small tree, 10-20 m high, spreading crown. Leaves essentially glabrous, occasionally having distant stellate trichomes on the lower surfaces, blades elliptic, 6-12 cm long, 3-5 cm broad, margins entire, the bases cuneately narrowed, apices acute to short acuminate; upper surfaces dark green, glossy; lower surfaces paler; finely reticulate on both surfaces, petioles 6-12 mm long with scattered lepidote trichomes. Flowers in axillary or terminal, semi-drooping, 3-6 flowered racemes, 2-5 cm long, pedicels 10-15 mm long, ferruginous, lepidote, minutely bracteolate at the base; calices 4-5 mm long, minutely toothed, ferruginous, lepidote; corolla lobes 12-15 mm long, oblong-elliptic, acute, with silvery lepidote pubescence; styles just shorter than corolla lobes; filaments about as long as anthers, both mixed with scattered, long, stellate trichomes, bases of filaments with tufts of long trichomes; style glabrous, about as long as corolla lobes; stigma 3-lobed. Drupes slightly asymmetrical, oblong-elliptic, 2.5-3.5 cm long, 13-15 cm wide, apices slightly acuminate, covered with crusty lepidote trichomes; seeds 18-22 mm long, 8-10 mm wide, pale reddish brown, faintly glossy, with three pale grooves running from the hilum sideward (Fig. 15).

The racemes and new branchlets are covered with lacerate, ferruginous, lepidote trichomes.

Styrax portoricensis, endemic to Puerto Rico and the only *Styrax* occurring there, is found on slopes along creeks and in mountainous regions. In the original description, Krug and Urban (1893) give the habitat in Puerto Rico as "in Sierra Juncos, de Naguabo et de Luquillo, in sylvis Primaevis, veris. Sept. Florif." (Fig. 21).

Holotype: PUERTO RICO. HUMACAO. Sierra de Naguabo in montis Piedra pelada. *Urban* 1169, 26 Apr 1885 (NY! isotypes: F! GH! MO! US!).

PUERTO RICO. HUMACAO. Sierra de Yabucoa, *Urban* 2661 (NY, US); Sierra de Naguabo, *Urban* 1169 (F, GH, MO, NY, US). Province unknown, Horu 309 (NY).

Styrax portoricensis is very distinct and not readily confused with any other *Styrax* included in this study. The leaves, thickened and with revolute margins, very much resemble those of *Quercus virginiana* of the southeastern United States. The flowers resemble those of *S. argenteus* in general morphology but have dense lepidote pubescence. The fruit are very distinct, by far the largest of any *Styrax* included herein.

14. *STYRAX GLABER* Swartz, Nov. Gen. et Spec. Plant. 74. 1788.

Styrax occidentalis Sw. ex Thunb. Diss. de Styrace. 8. 1813.

Small to medium sized tree, 6–18 m tall. Leaves elliptical or elliptical-oblong, blades 8–15 cm long, 3.5–5.5 cm broad, margins subentire, the bases cuneate, apices short to long acuminate; upper surfaces glabrous, smooth to slightly coriaceous; lower surfaces covered with pale lepidote-stellate pubescence; petioles 12–14 mm long, lepidote-stellate. Flowers in axillary, semi-drooping, 4–7 flowered racemes, 2.5–3.5 cm long; pedicels 9–14 mm long, lepidote-stellate, with minute bracts basally; calices 5–6 mm long, truncate, minutely toothed, lepidote-stellate; corolla lobes 16–18 mm long, oblong-linear, acute, covered with matted lepidote-stellate pubescence; stamens 3 mm shorter than corolla lobes, anthers 2/5 this length; filaments bearded basally with long trichomes, glabrous upwards; style glabrous, barely longer than the stamens; stigma 3-lobed. Drupes ovoid to globose-ovoid, 2 cm long, 1 cm wide, style basally persistent; seeds usually 1, smooth, pale brown (Fig. 16).

Styrax glaber occurs on moist slopes throughout the Windward Islands, ranging through Guadeloupe, Martinique, Saint Lucia, and Tobago. It is also recorded from Trinidad (Fig. 21).

Holotype: BRITISH WEST INDIES. Willdenow 8326 (B; photograph of holotype examined).

WEST INDIES. GUADELOUPE. Bois de Bains-Tames, *Pere Duss* 3263 (F, NY, US).

MARTINIQUE. Herbier de la Martinique, *Pere Duss* 1900 (US); 1728 (F, MO, NY, US).

ST. LUCIA. Barre de L'Ile, Beard 510 (MO, NY, UNC); Barre de L'Ile, Beard 1113 (GH, MO, NY).

TOBAGO. Orxborough, Cowan 1413 (NY).

Styrax glaber is the only *Styrax* occurring in the British West Indies. Perkins (1902) described a new variety, *S. glaber* var. *micranthus*, from Trinidad. It is, of course, possible that it is a "good" taxon and that it may intergrade with material from South America. Urban (1892) mentions the range of *S. glaber* (var. *glaber*) to include Trinidad. Since Perkins was a notorious "splitter" and since I have not seen the type material or any oth-

er specimen of var. *micranthus*, it is not recognized in this study.

Grisebach (1864) lists *S. guianensis*, found in Guiana and equatorial Brazil, as a synonym of *S. glaber*. This may be the entity that Perkins calls var. *micranthus*. In any event, further study of South American *Styrax* is necessary to establish the relationship between these taxa and *S. glaber* of the British West Indies.

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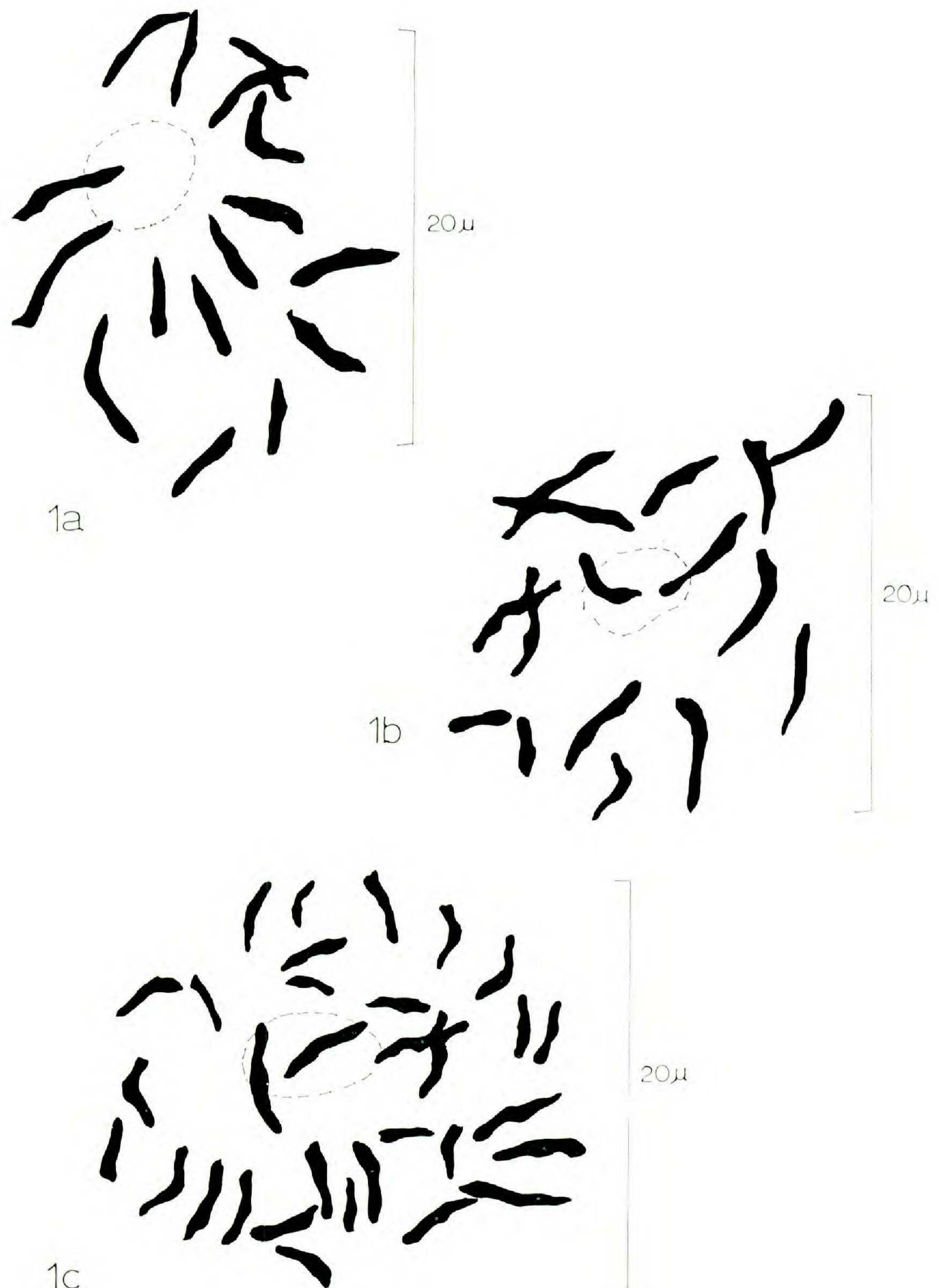


Fig. 1. Early prophase I in pollen mother cells: a. *Styrax americana* var. *americana*; b. *S. americana* var. *pulverulenta*; c. *S. grandifolia*.

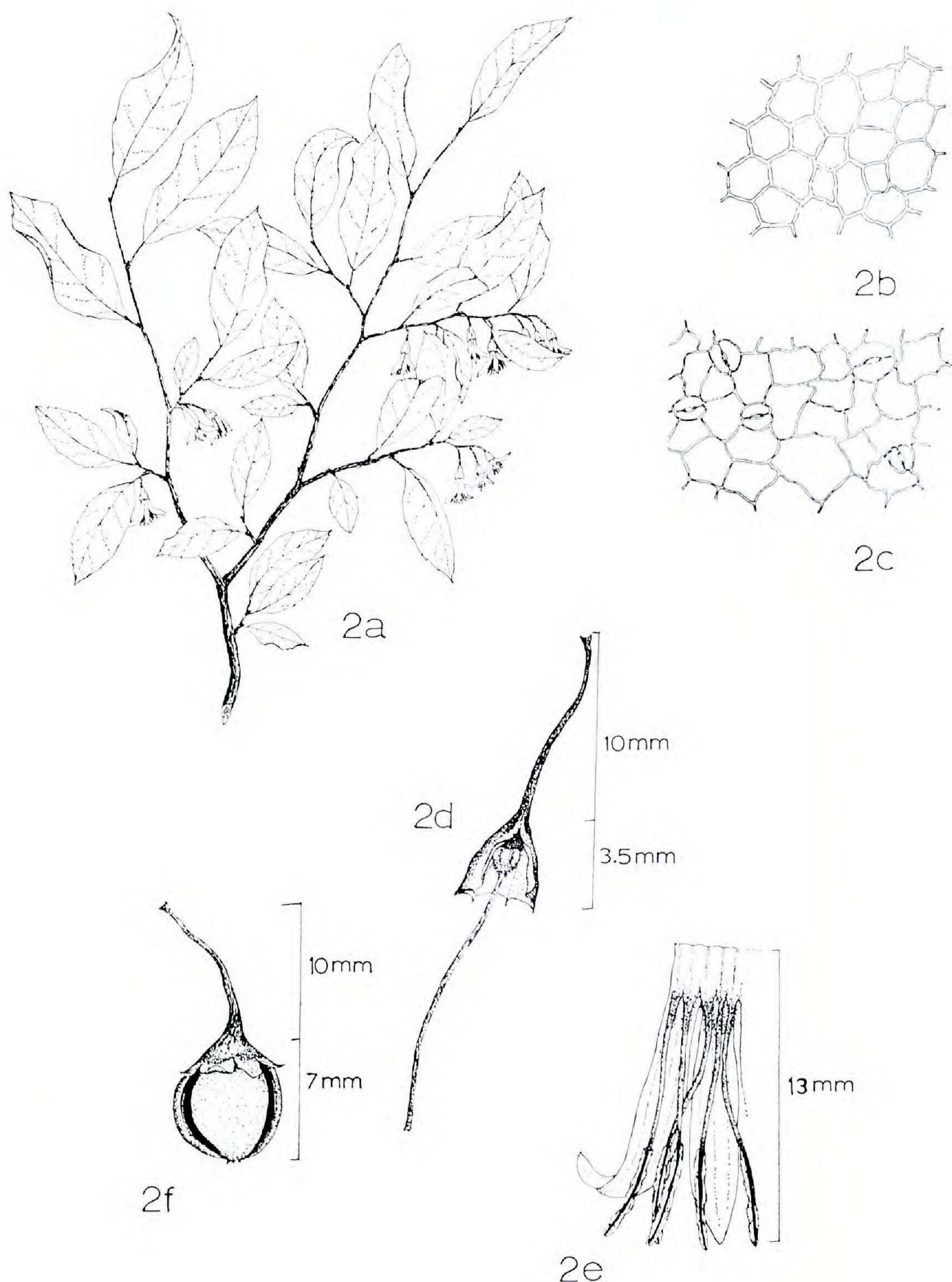
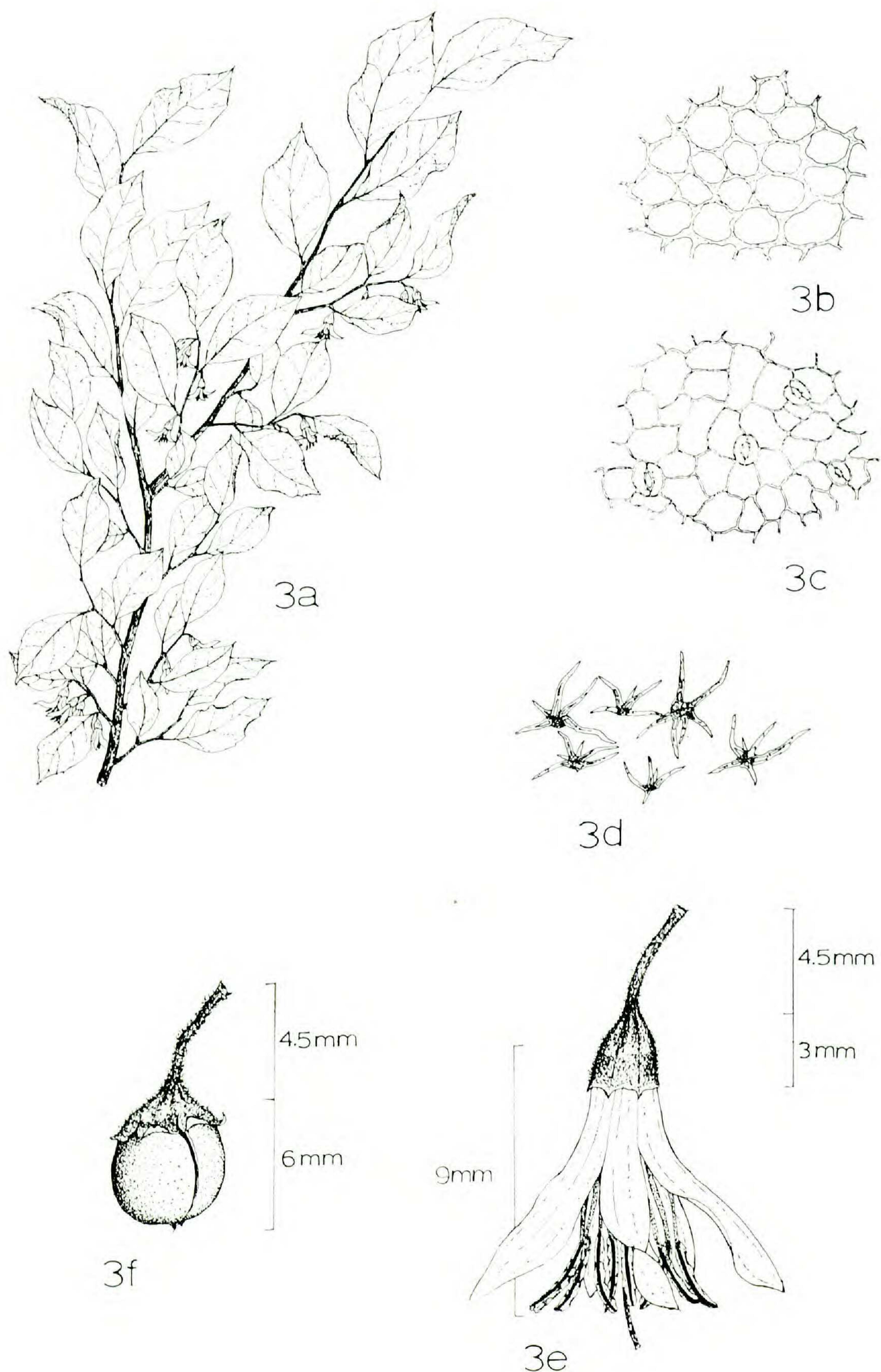


Fig. 2. *Styrax americana* var. *americana*: a. habit sketch; b, c. upper & lower leaf epidermis ($500\times$); d, e. mature flower parts; f. mature fruit.



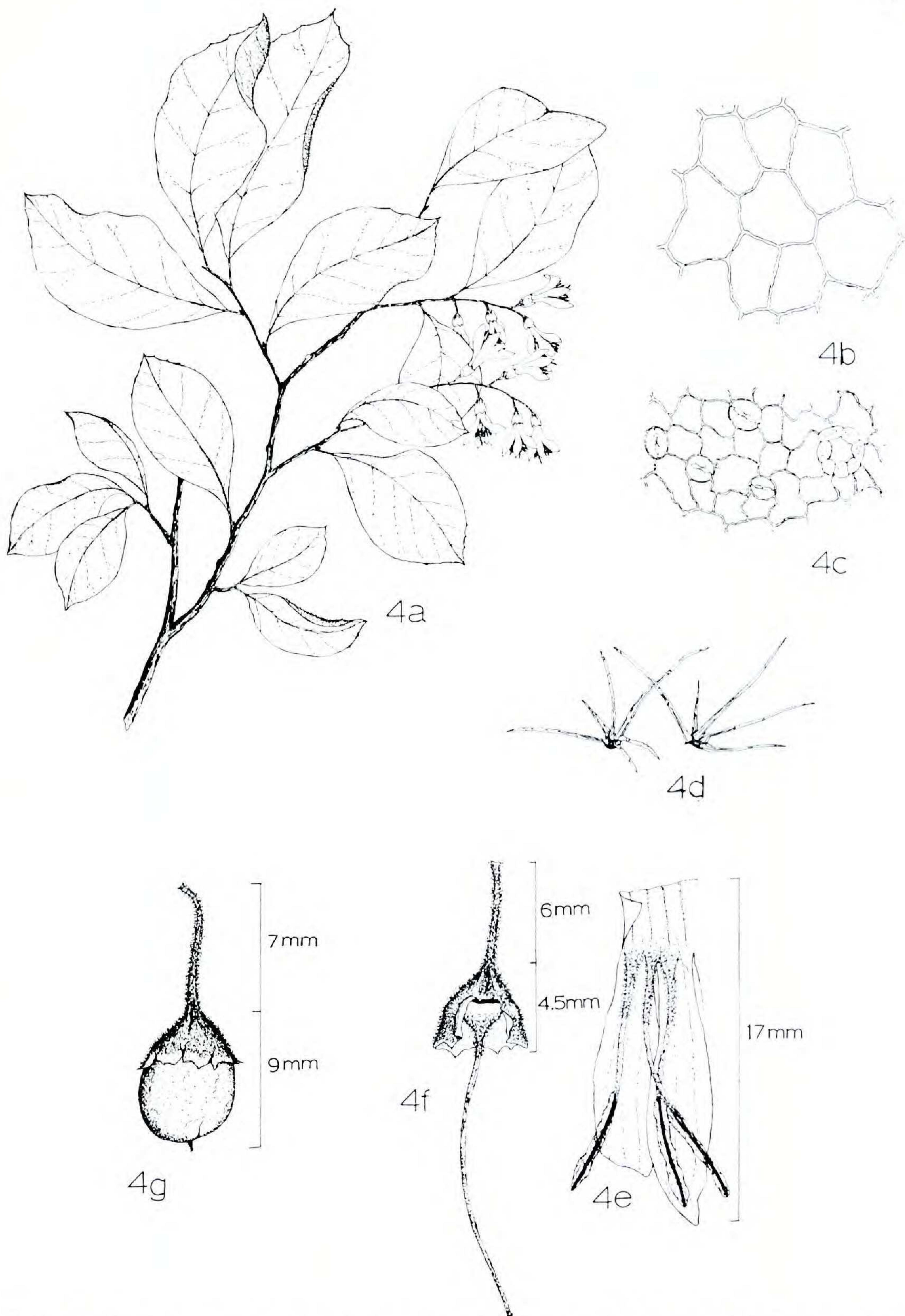


Fig. 3. *Styrax americana* var. *pulverulenta*: a. habit sketch; b, c. upper & lower leaf epidermis (500 \times); d. trichomes on lower leaf surface (128 \times); e. mature flower; f. mature fruit.

Fig. 4. *Styrax grandifolia*: a. habit sketch; b, c. upper & lower leaf epidermis (500 \times); d. trichomes on lower leaf surface (128 \times); e, f. mature flower parts; g. mature fruit.

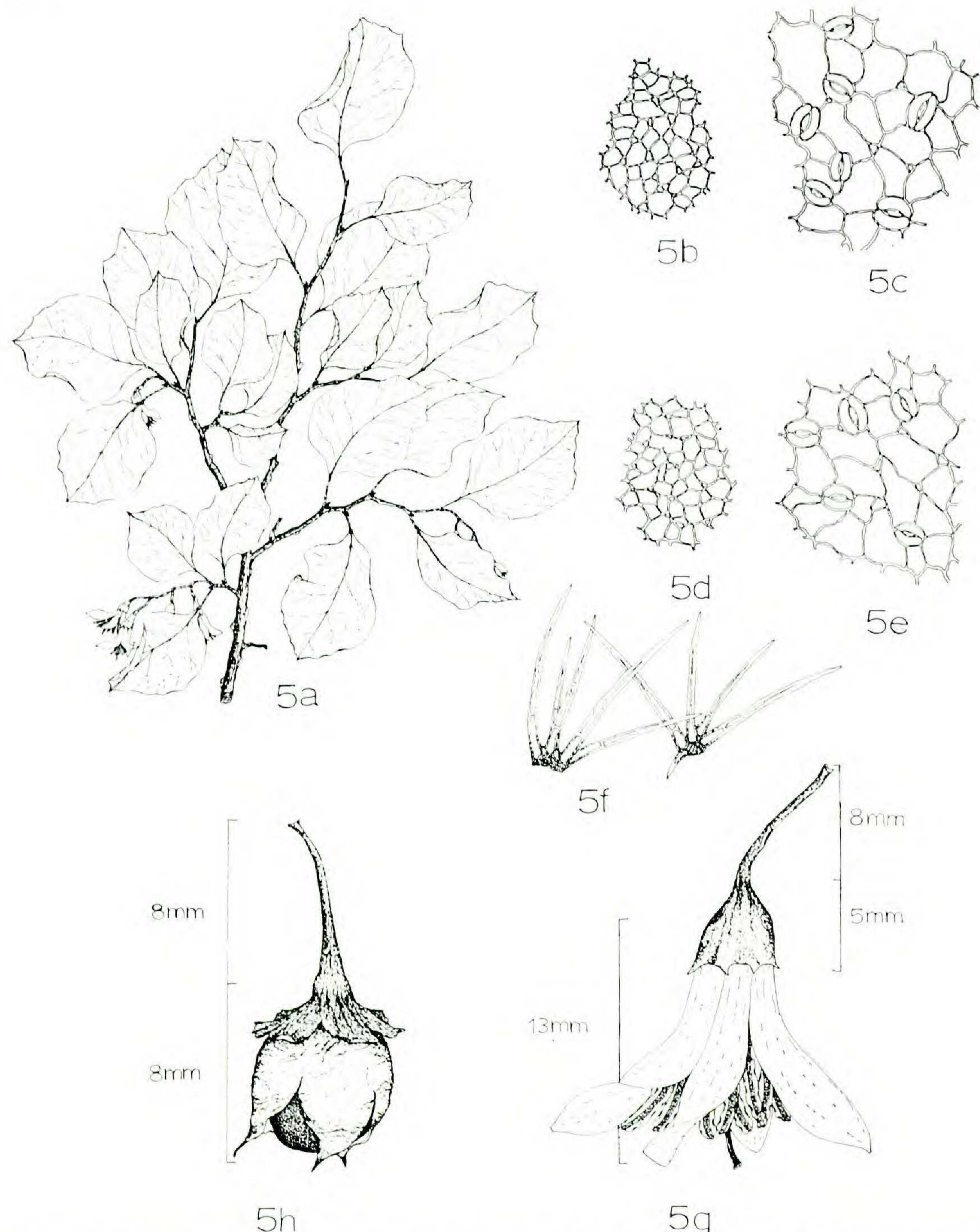
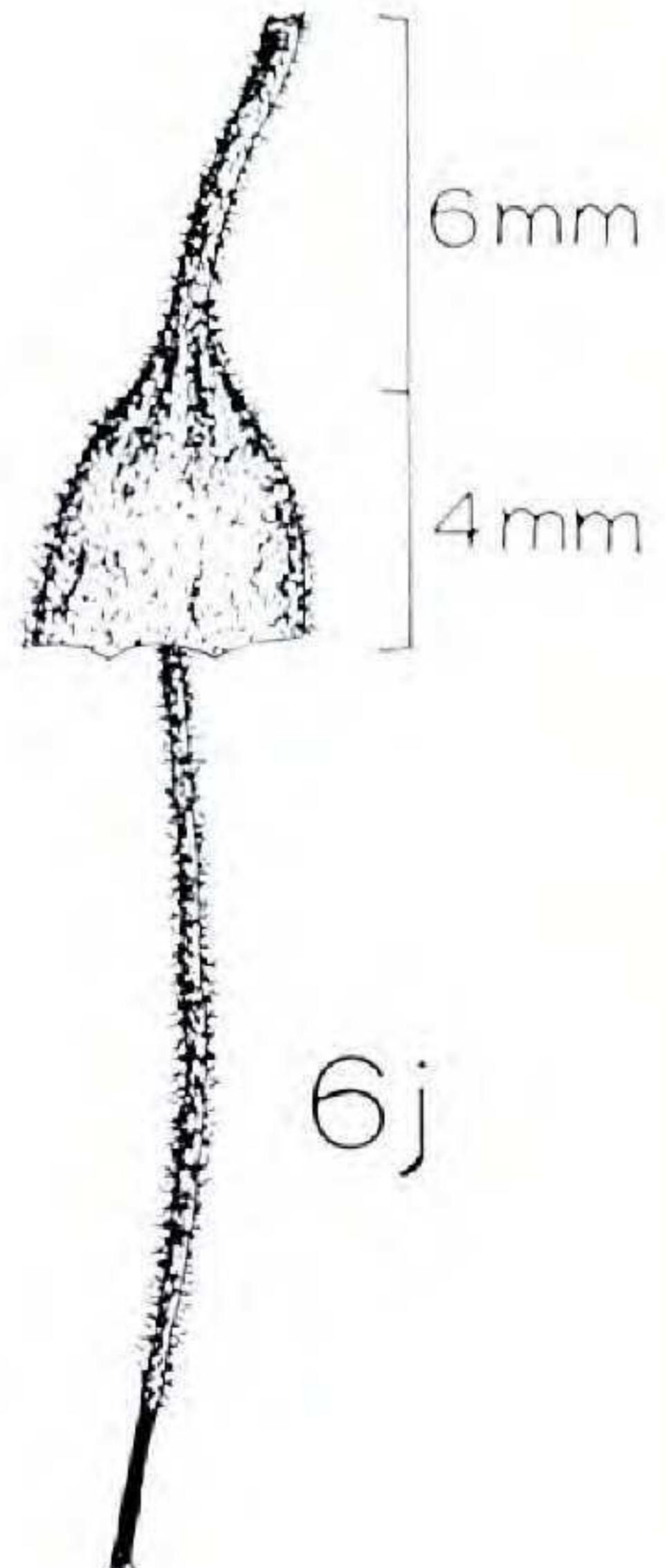
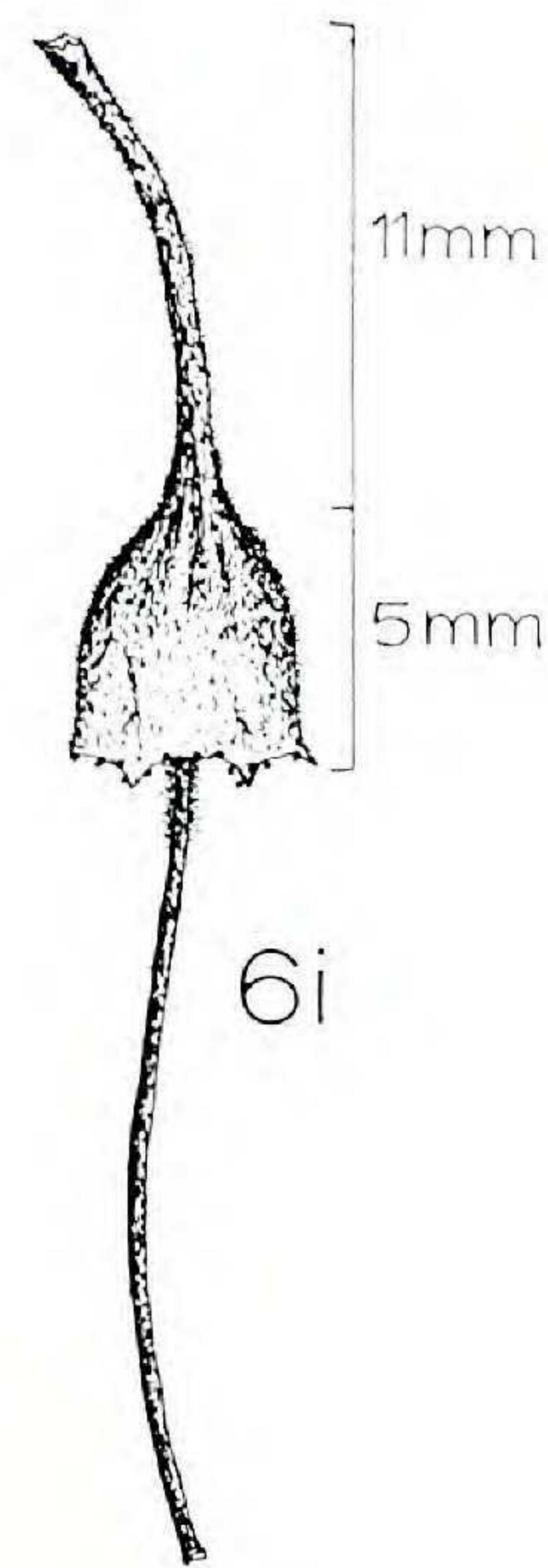
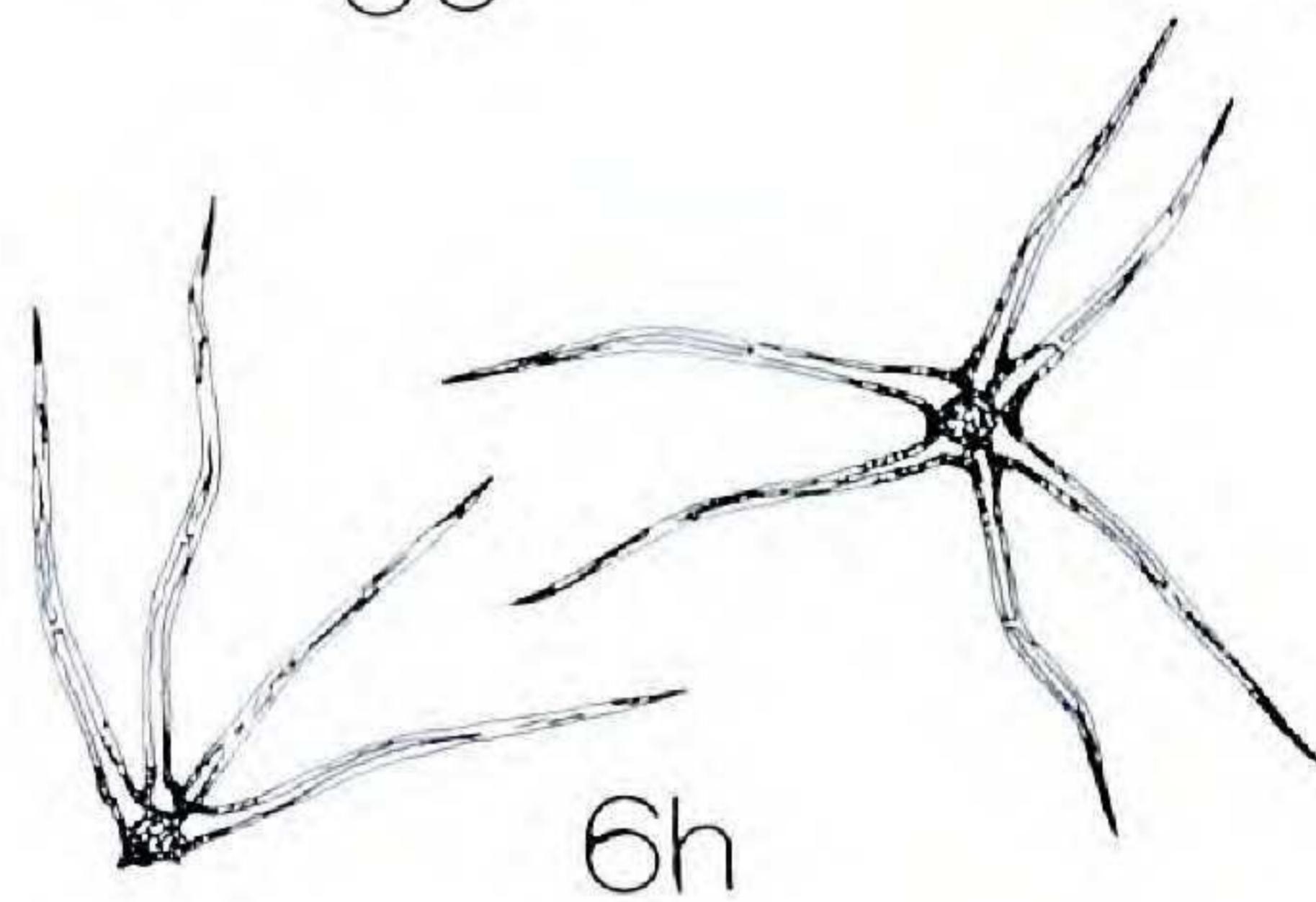
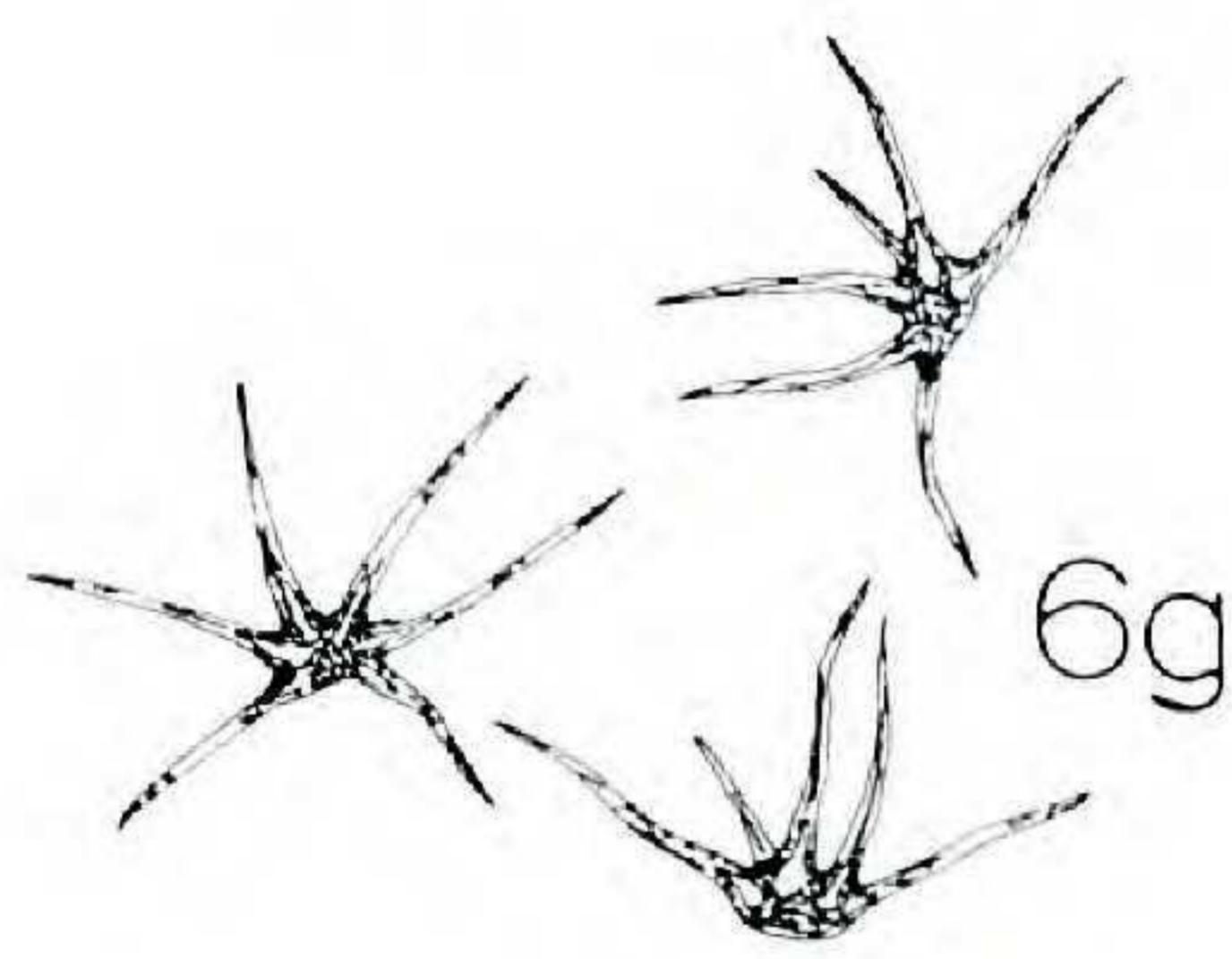
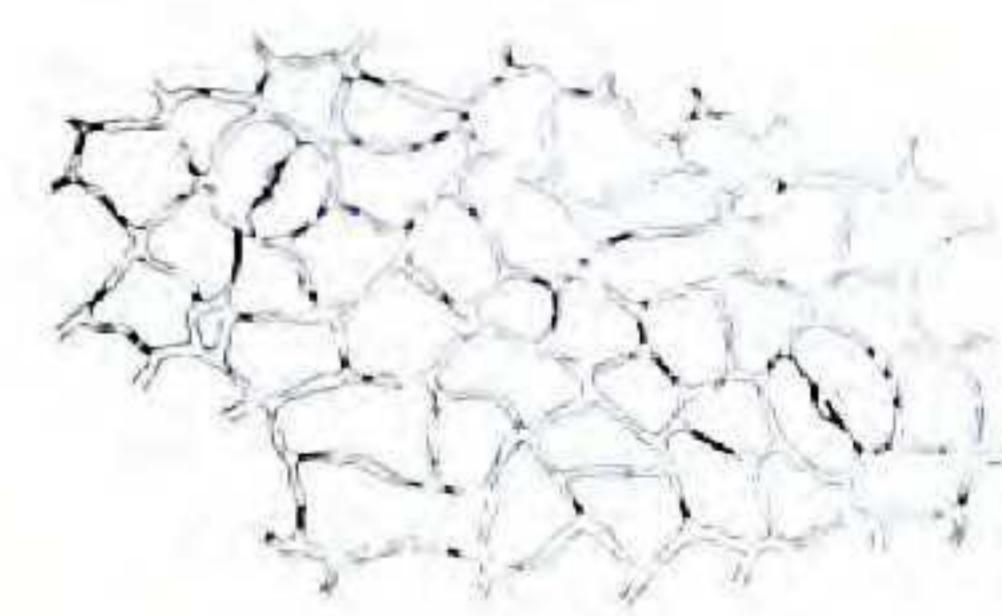
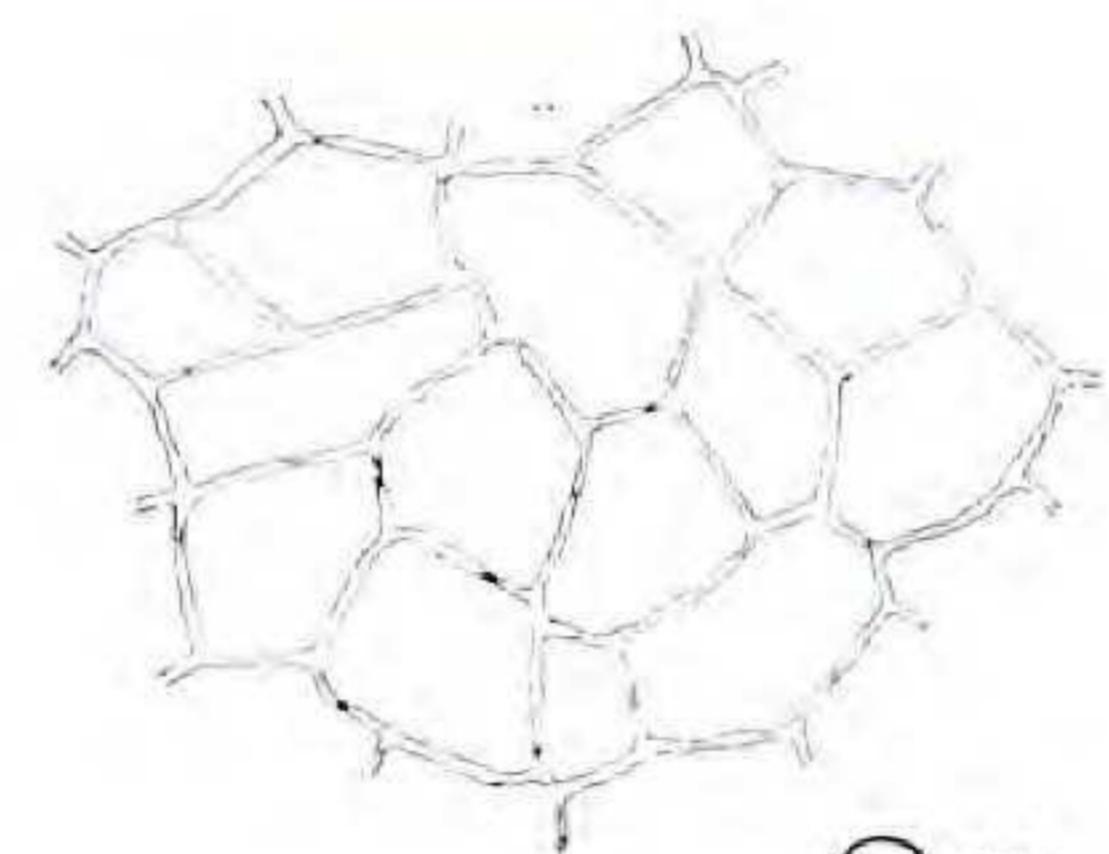
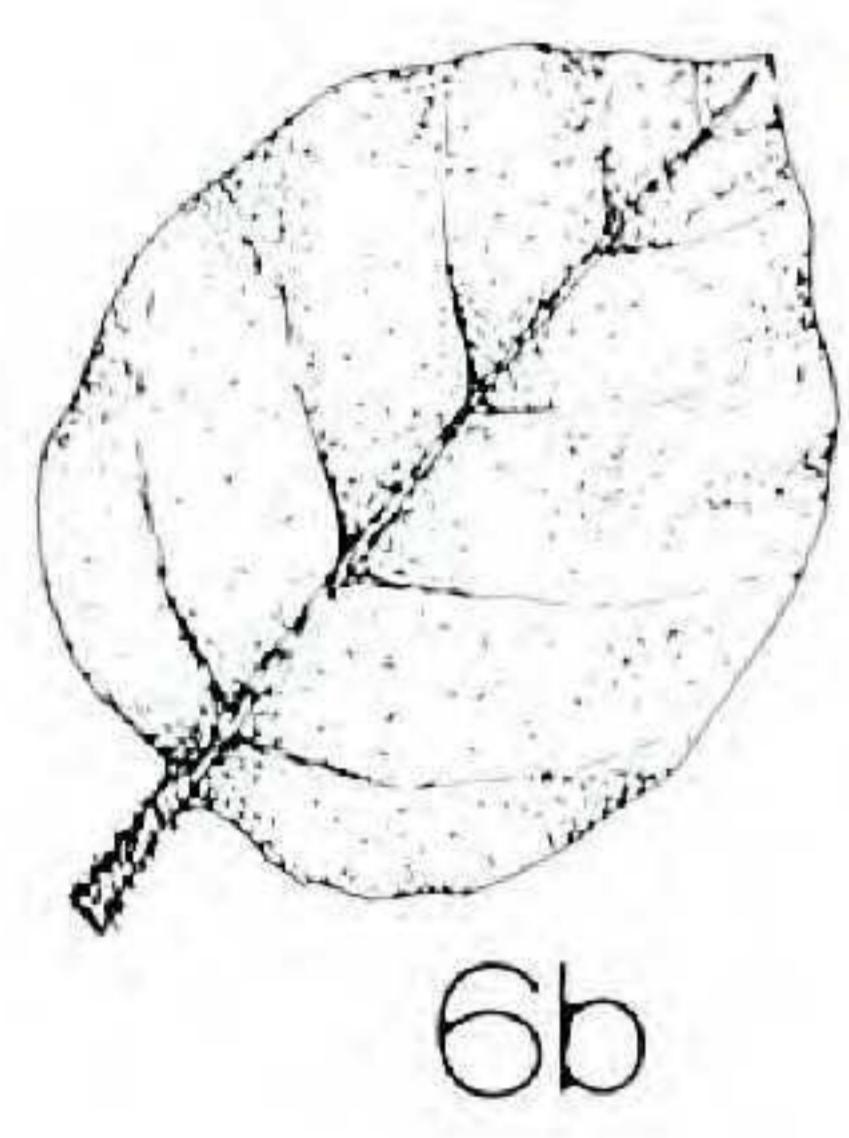
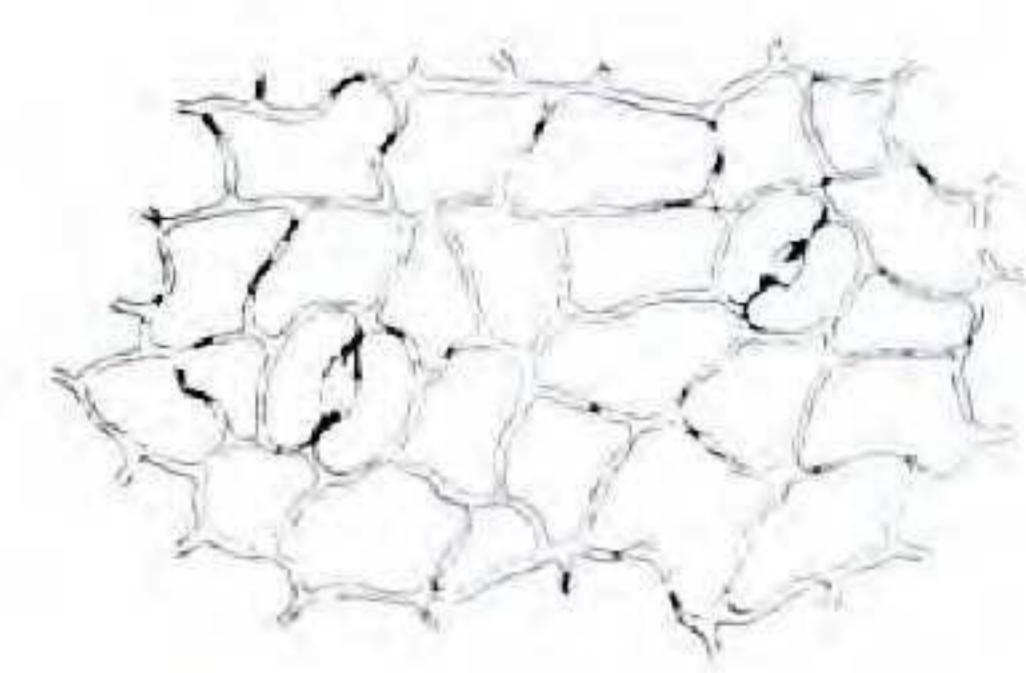
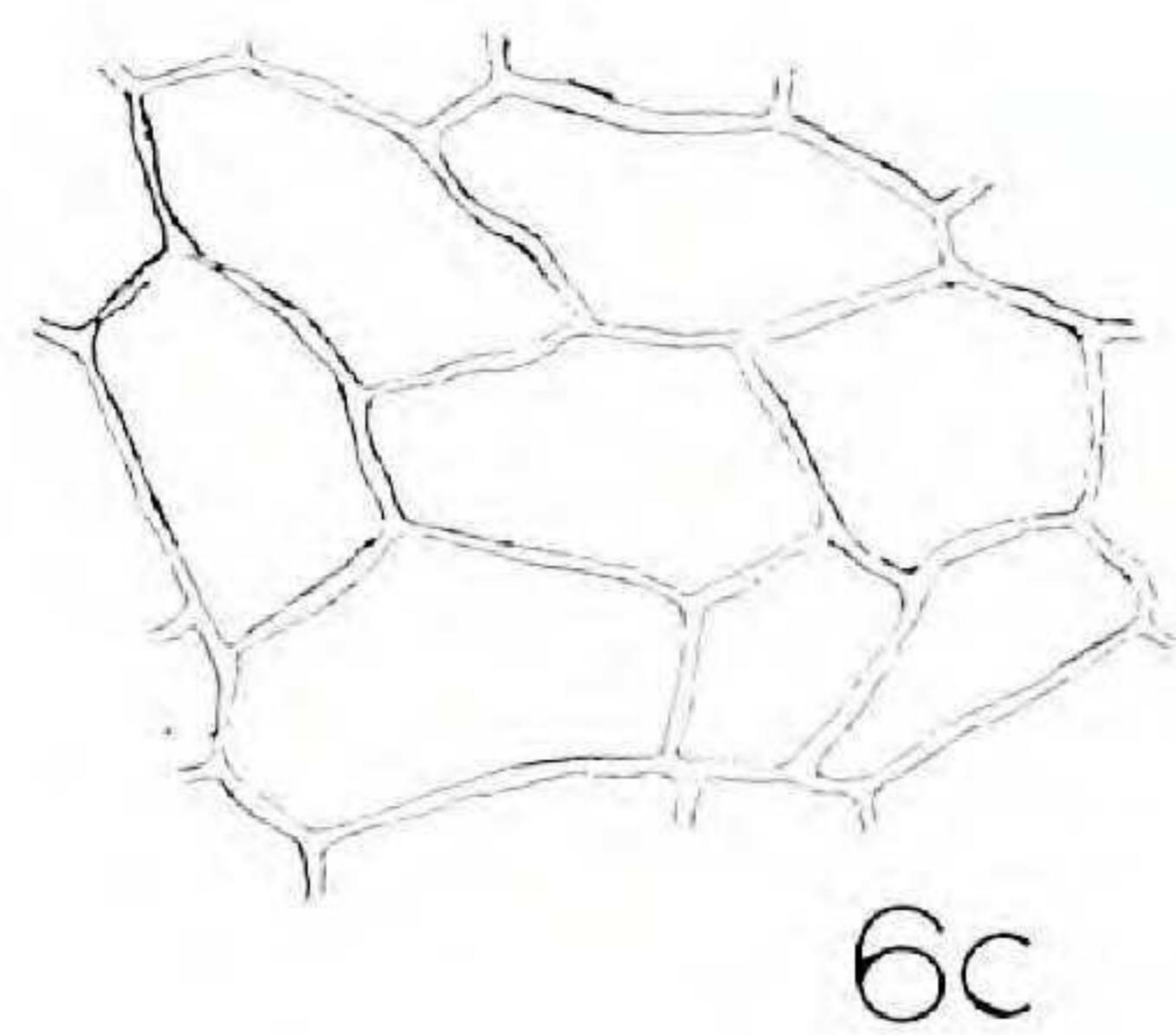
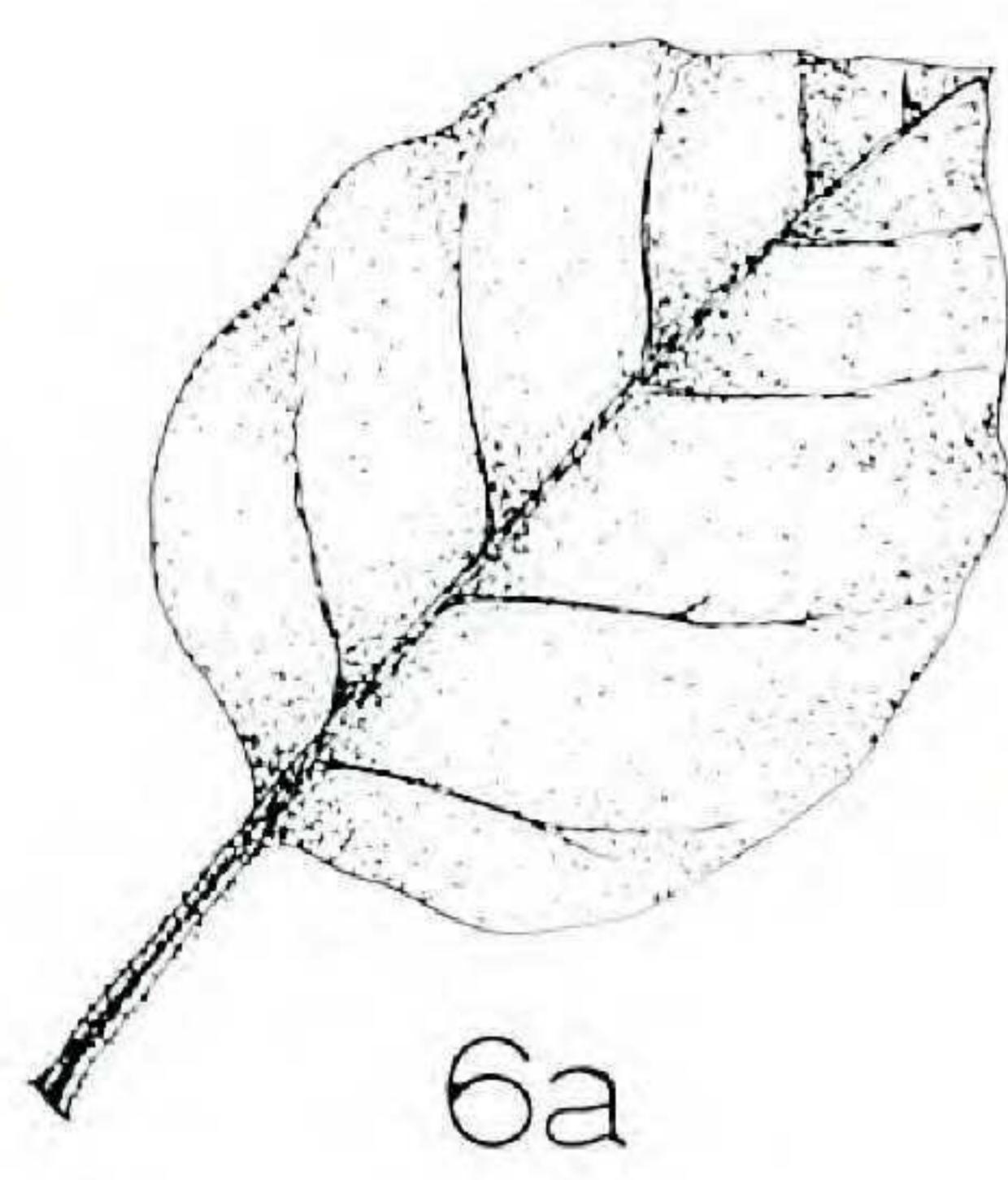


Fig. 5. *Styrax platanifolia*: a. habit sketch; b, c. upper & lower leaf epidermis of var. *platanifolia* ($500\times$); d, e. upper & lower leaf epidermis of var. *stellata* ($500\times$); f. trichomes on lower leaf surface of var. *stellata* ($128\times$); g. mature flower; h. mature fruit.

Fig. 6. *Styrax texana*, *S. youngae*: a. leaf of *S. texana*; b. leaf of *S. youngae*; c, d. upper & lower leaf epidermis of *S. texana* ($500\times$); e, f. upper & lower leaf epidermis of *S. youngae* ($500\times$); g. trichomes on lower leaf surface of *S. texana* ($128\times$); h. trichomes on lower leaf surface of *S. youngae* ($128\times$); i. calyx & pistil of *S. texana*; j. calyx & pistil of *S. youngae*.



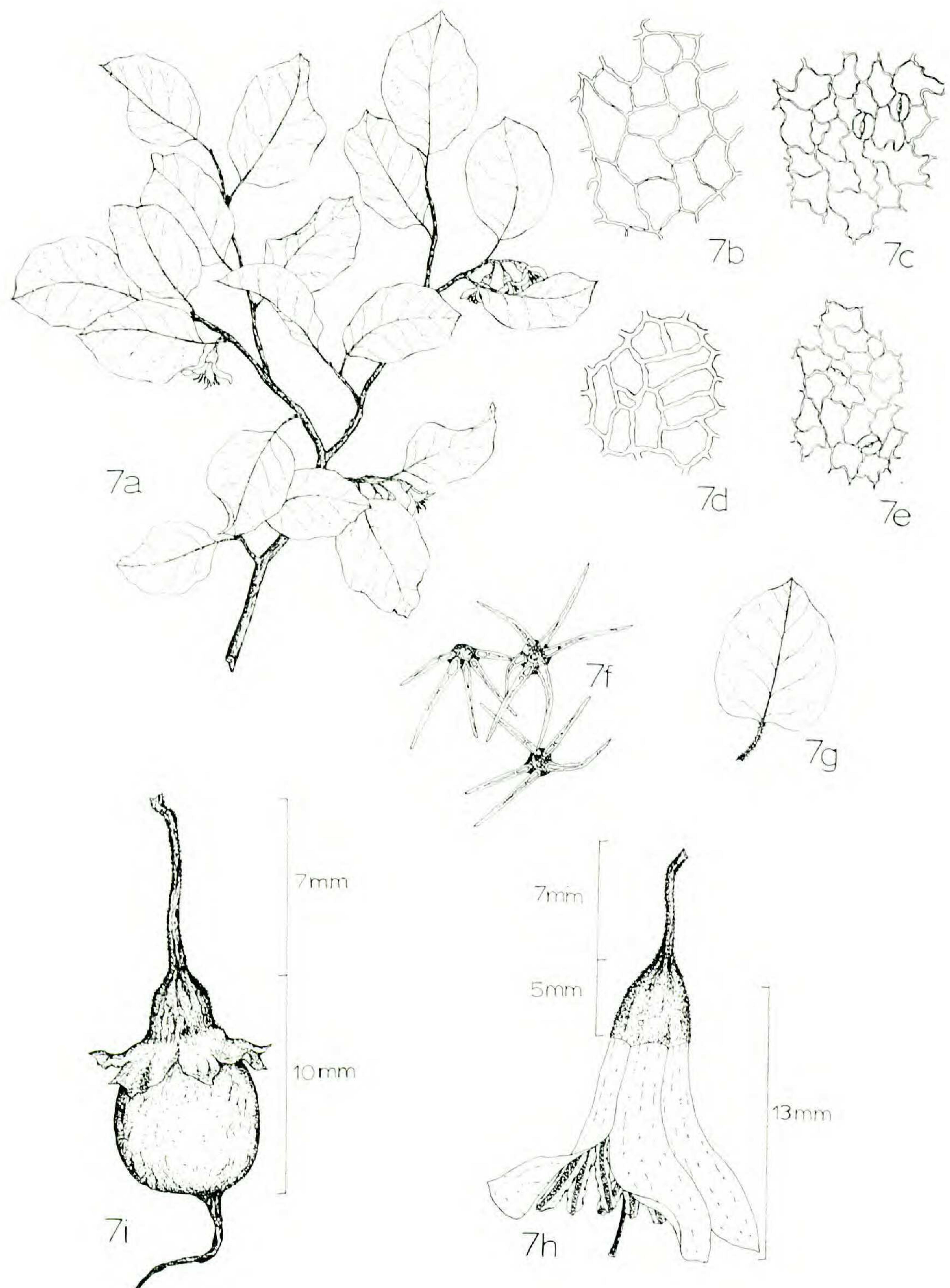


Fig. 7. *Styrax officinalis*: a. habit sketch of var. *californica*; b. c. upper & lower leaf epidermis of var. *californica* ($500\times$); d, e. upper & lower leaf epidermis of var. *fulvescens* ($500\times$); f, g. trichomes on lower leaf surface ($128\times$), and leaf of var. *fulvescens*; h. mature flower; i. mature fruit.

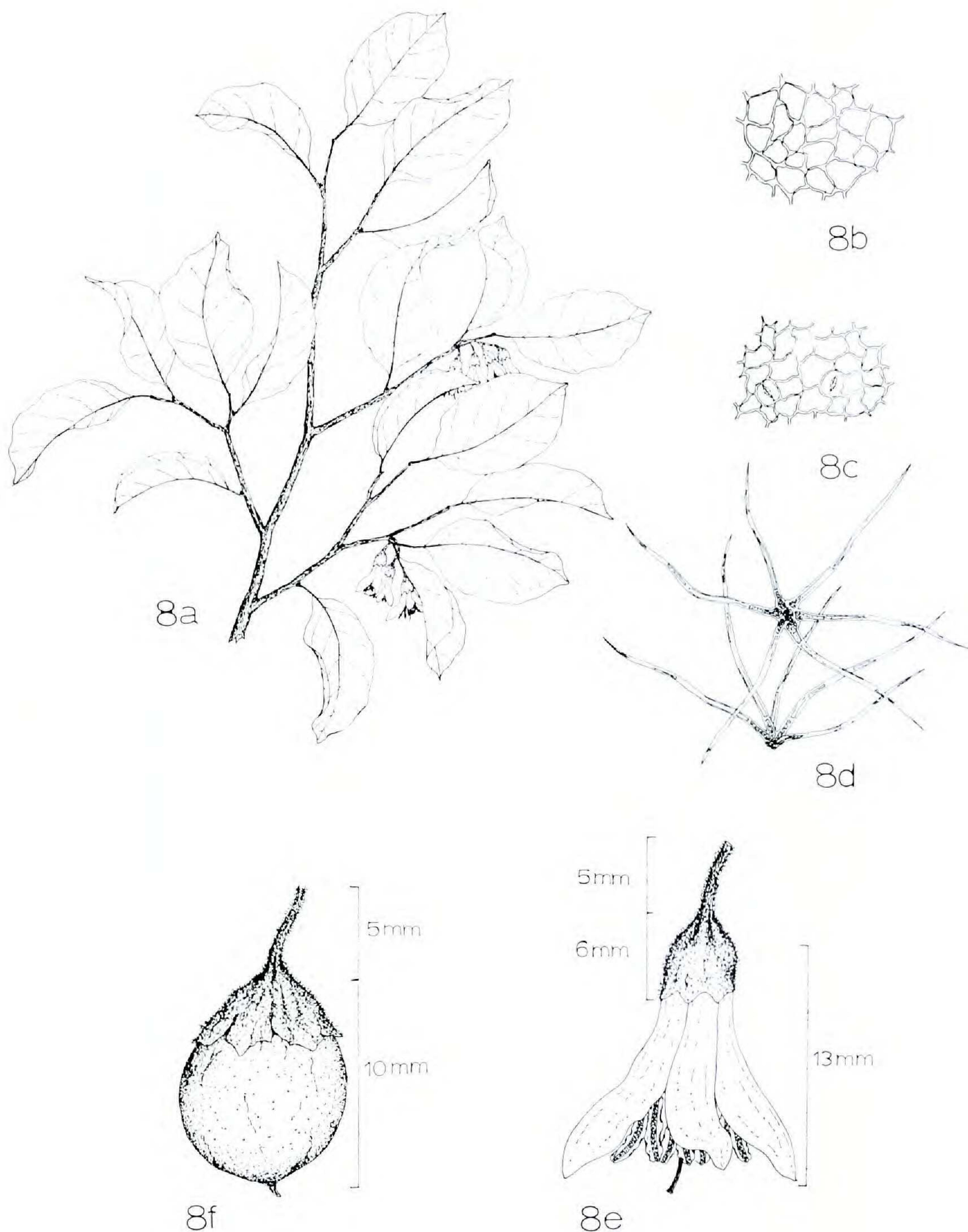


Fig. 8. *Styrax jaliscana*: a habit sketch; b, c. upper & lower leaf epidermis (500 \times); d. trichomes on lower leaf surface (128 \times); e. mature flower; f. mature fruit.

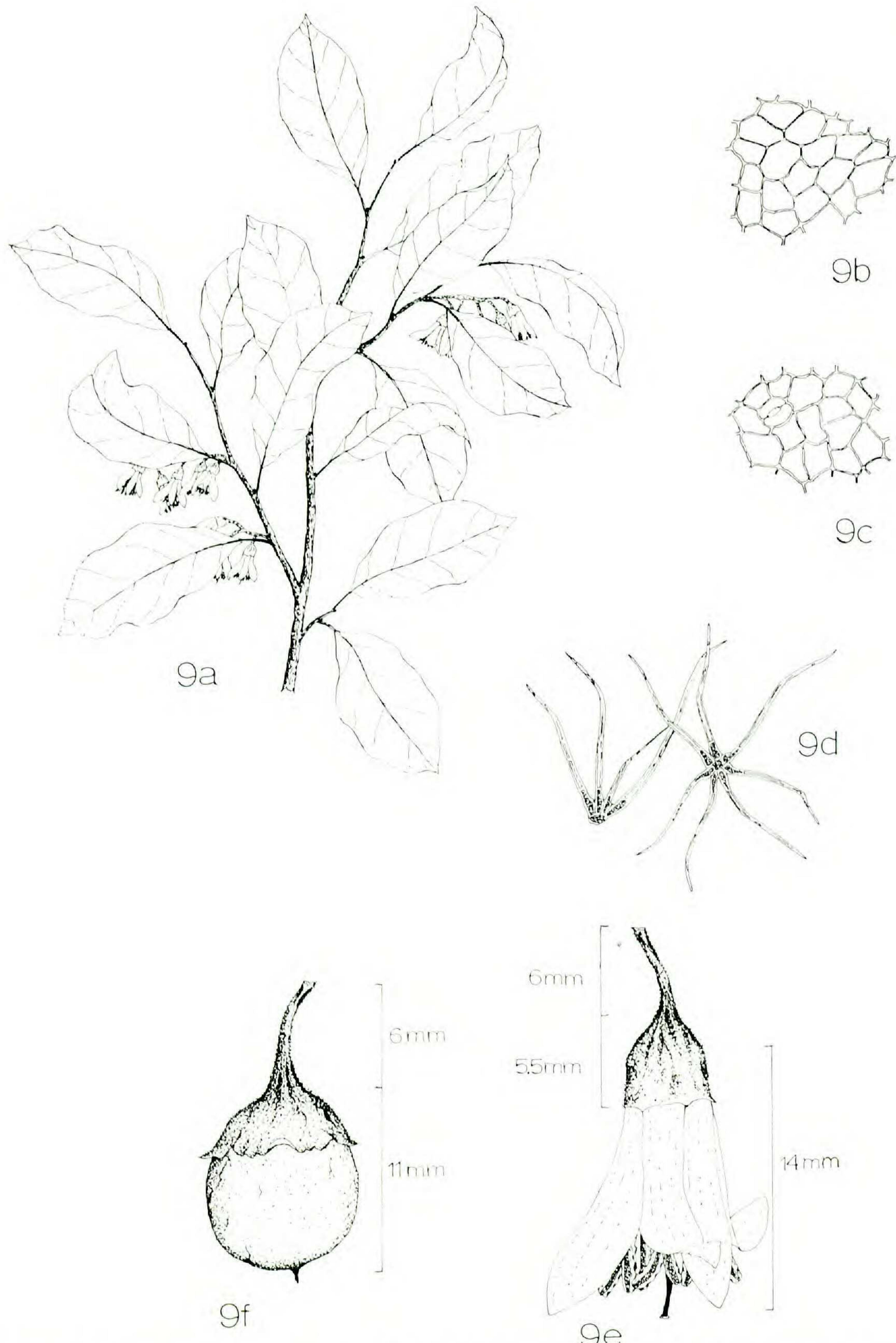


Fig. 9. *Styrax glabrescens*: a. habit sketch; b, c. upper and lower leaf epidermis ($500\times$); d. trichomes on lower leaf surface of var. *pilosus* ($128\times$); e. mature flower; f. mature fruit.

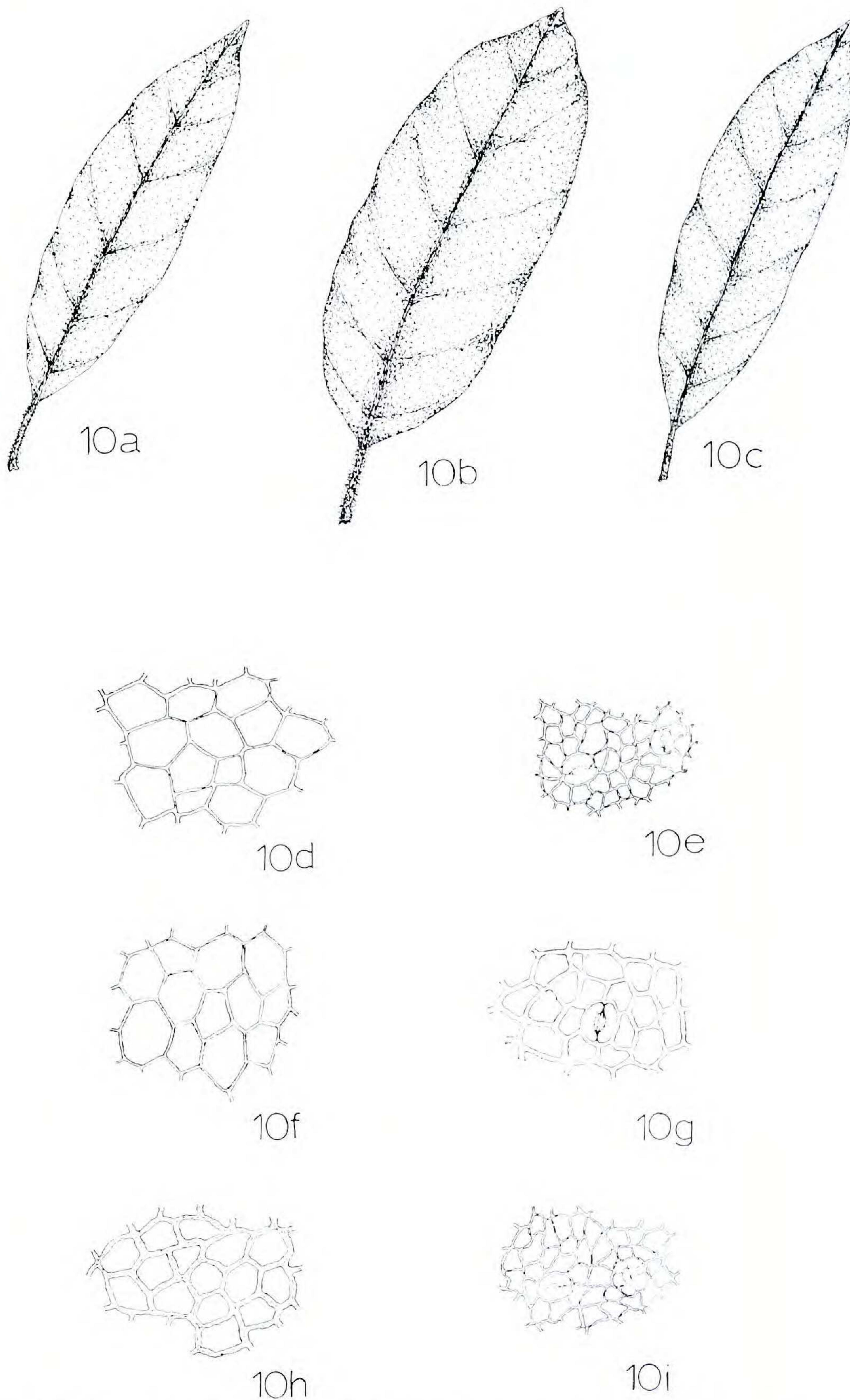
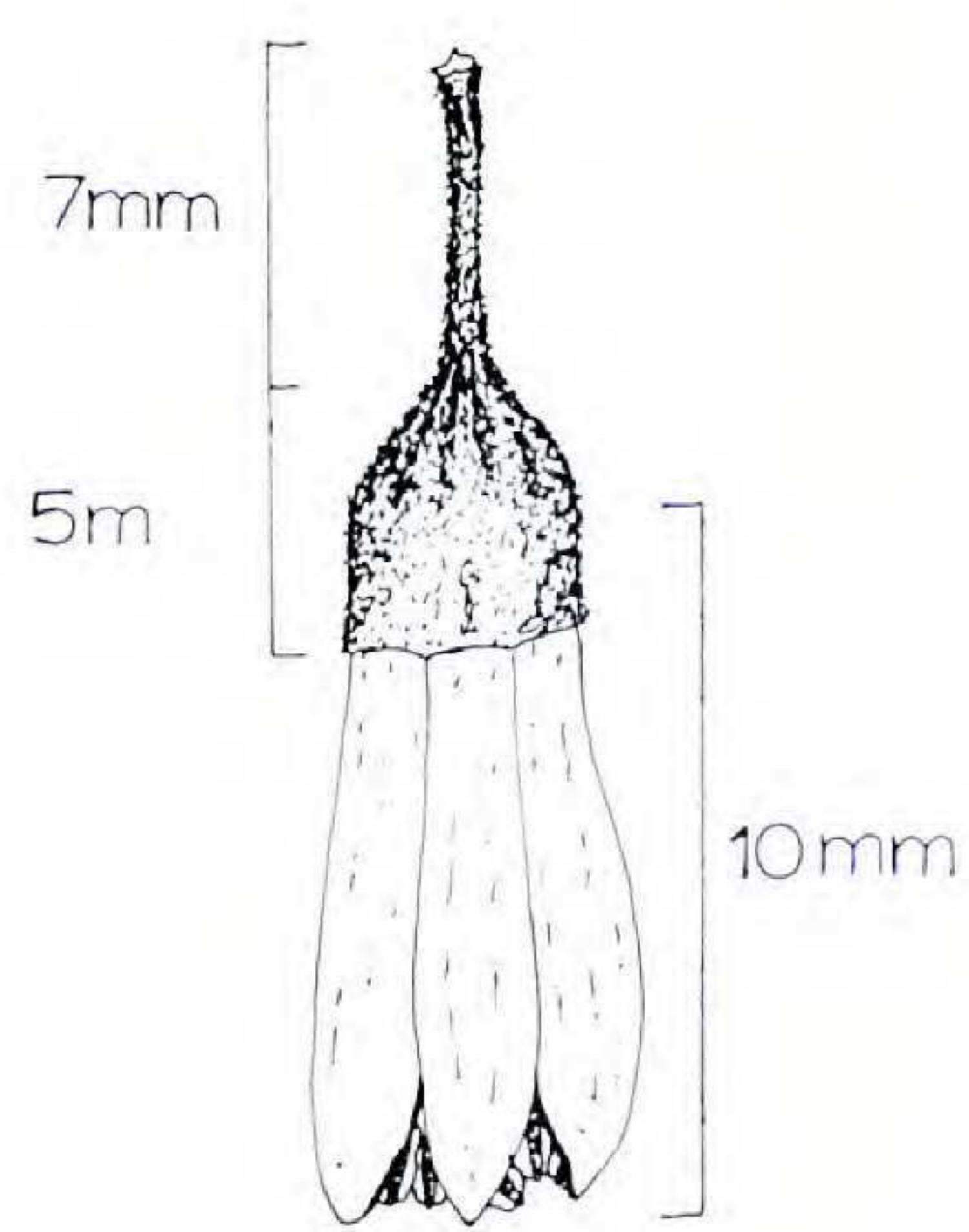
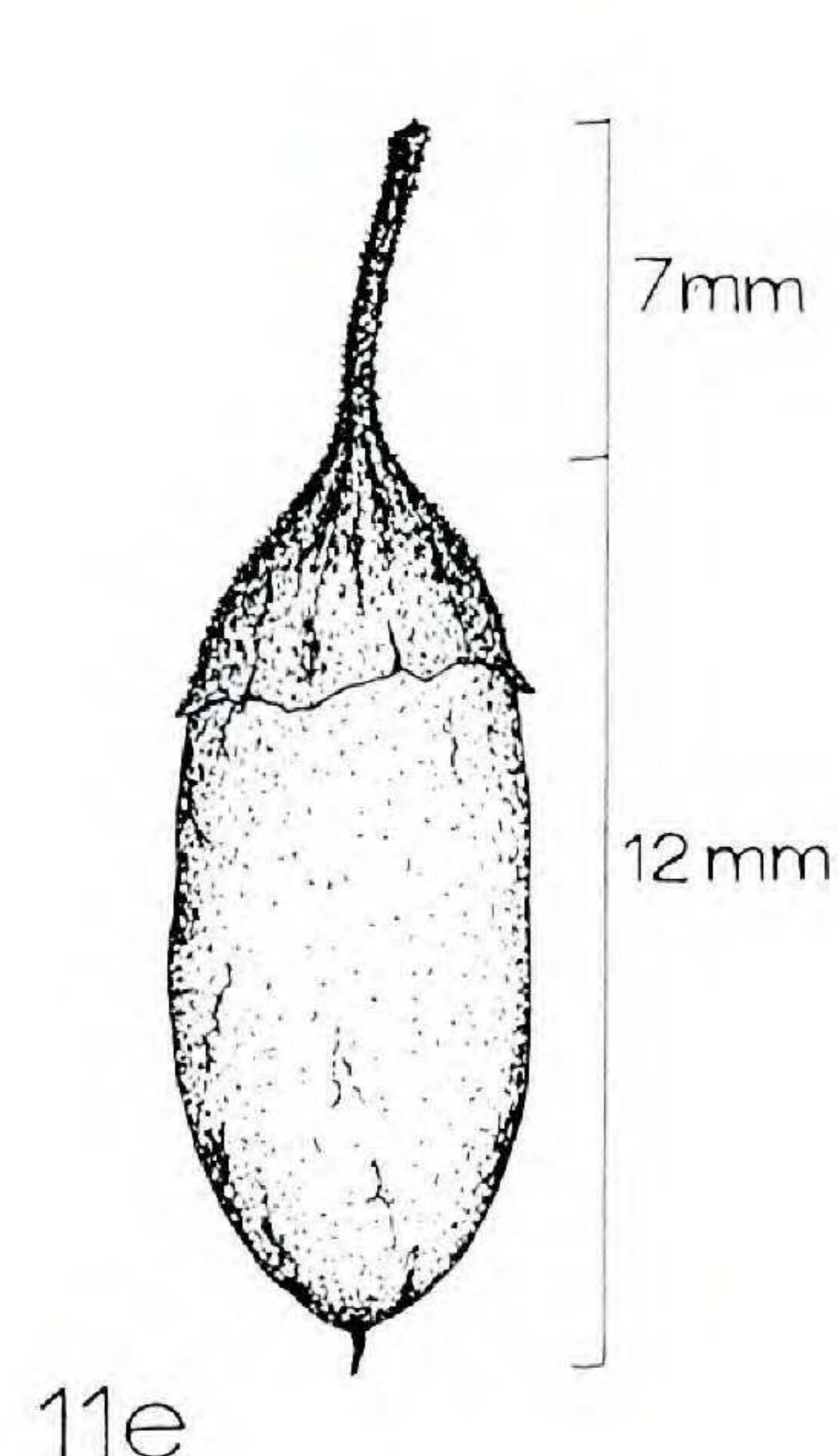
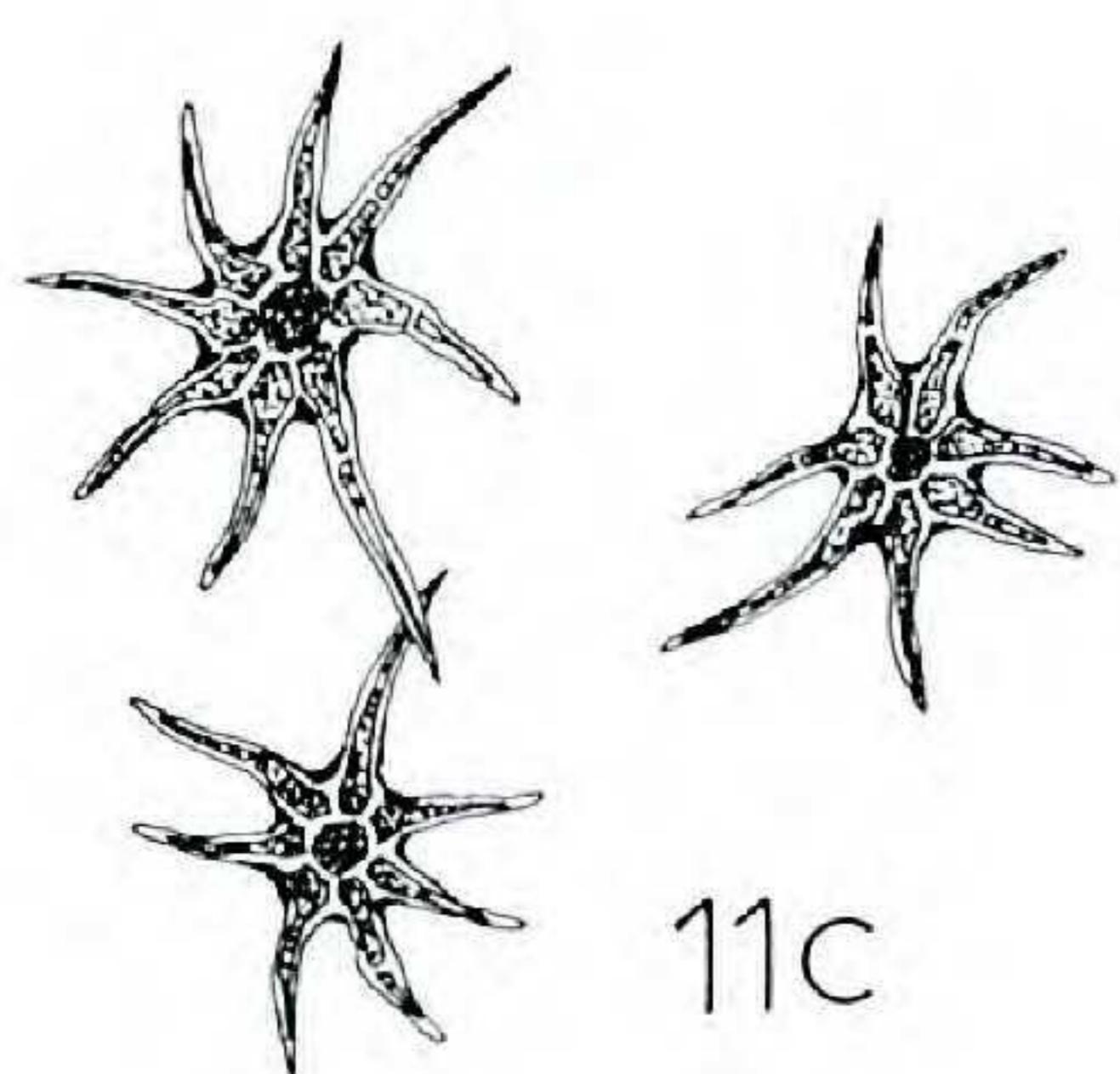
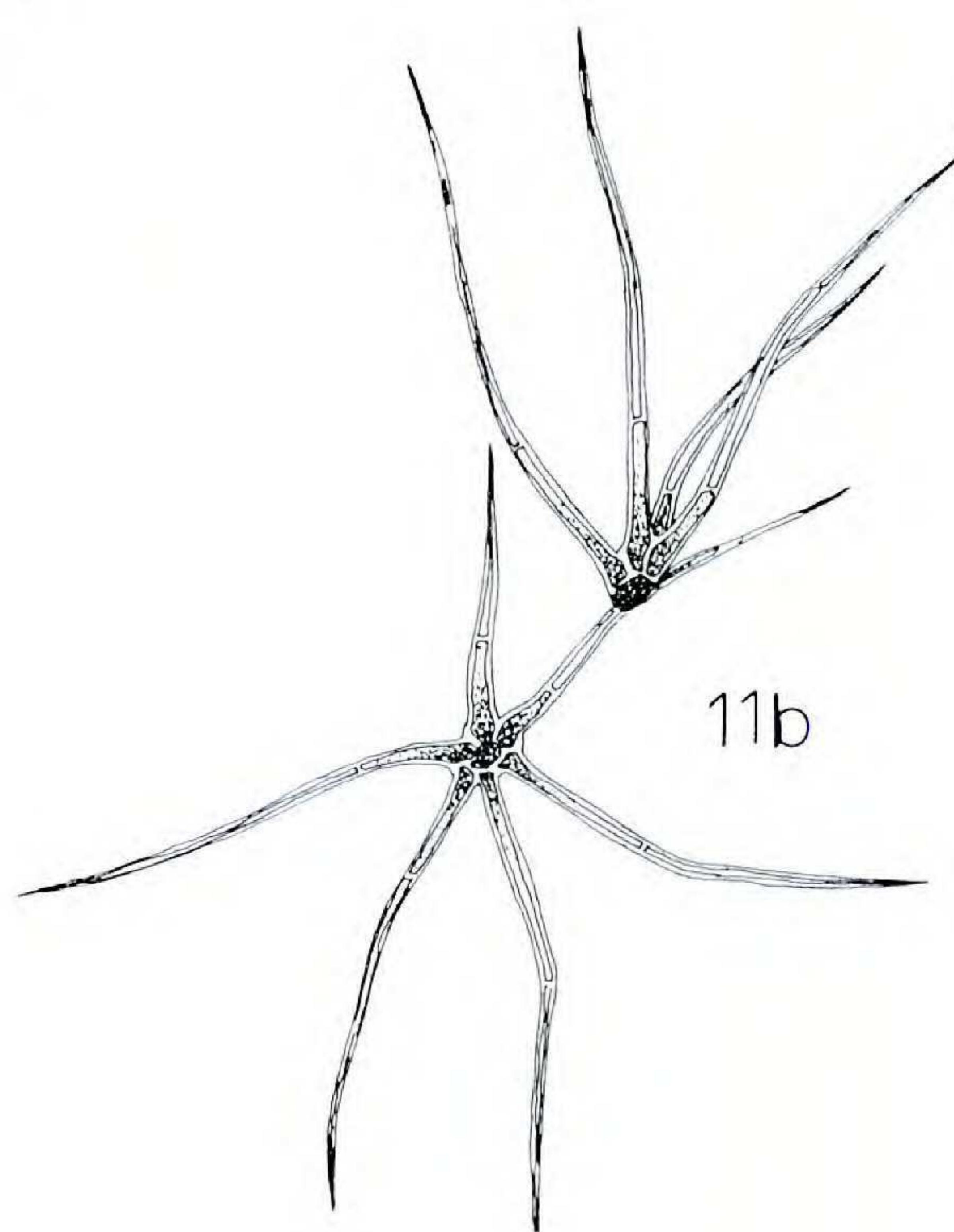
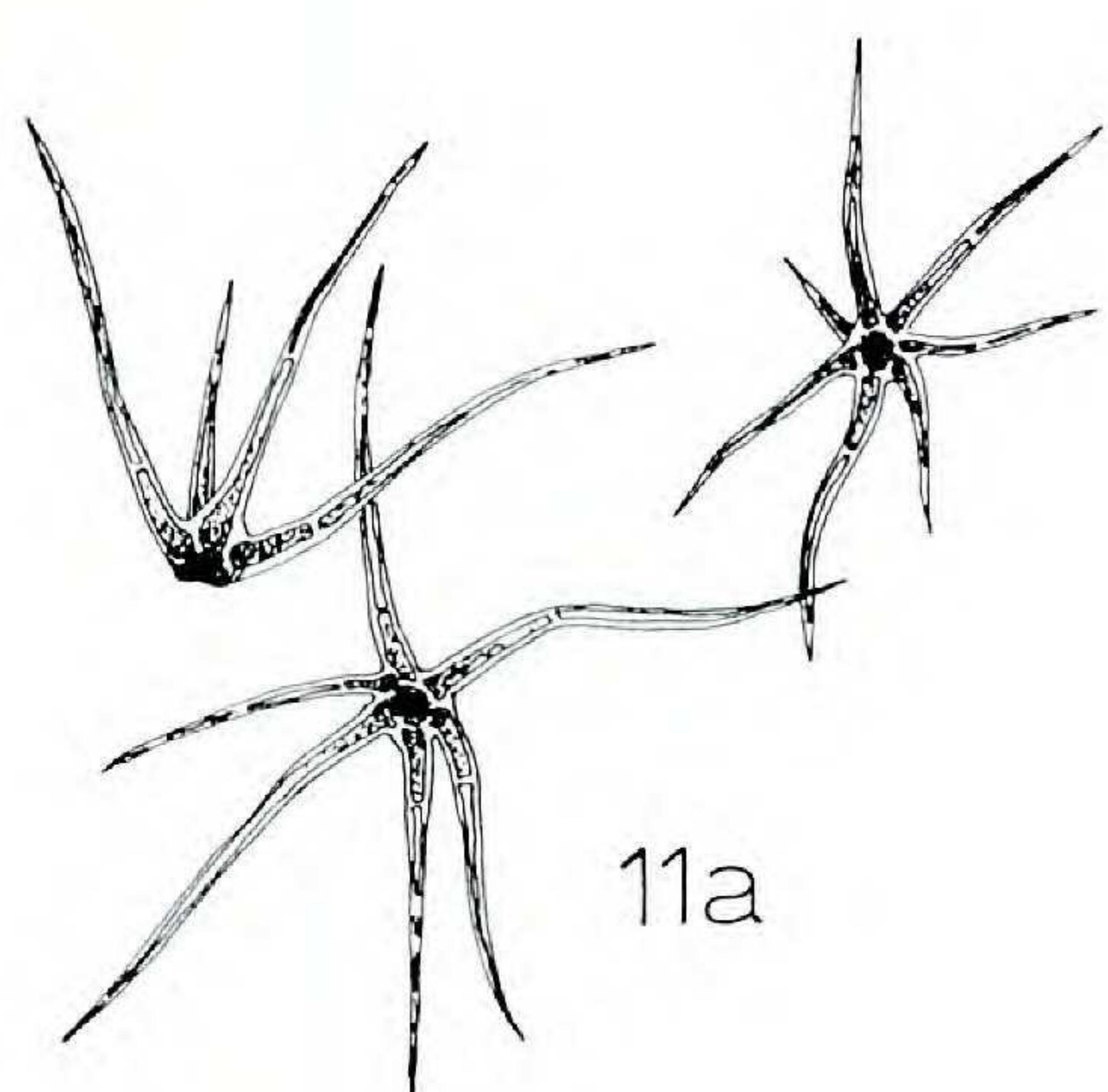


Fig. 10. *Styrax argenteus*: a. leaf of var. *argenteus*; b. leaf of var. *hintonii*; c. leaf of var. *ramirezii*; d, e. upper & lower leaf epidermis of var.

argenteus (500 \times); f, g. upper & lower leaf epidermis of var. *hintonii* (500 \times); h, i. upper & lower leaf epidermis of var. *ramirezii* (500 \times).

Fig. 11. *Styrax argenteus*: a. trichomes on lower leaf surface of var. *argenteus* (128 \times); b. trichomes on lower leaf surface of var. *hintonii* (128 \times); c. trichomes on lower leaf surface of var. *ramirezii* (128 \times); d. mature flower of var. *argenteus*; e. mature fruit of var. *argenteus*.



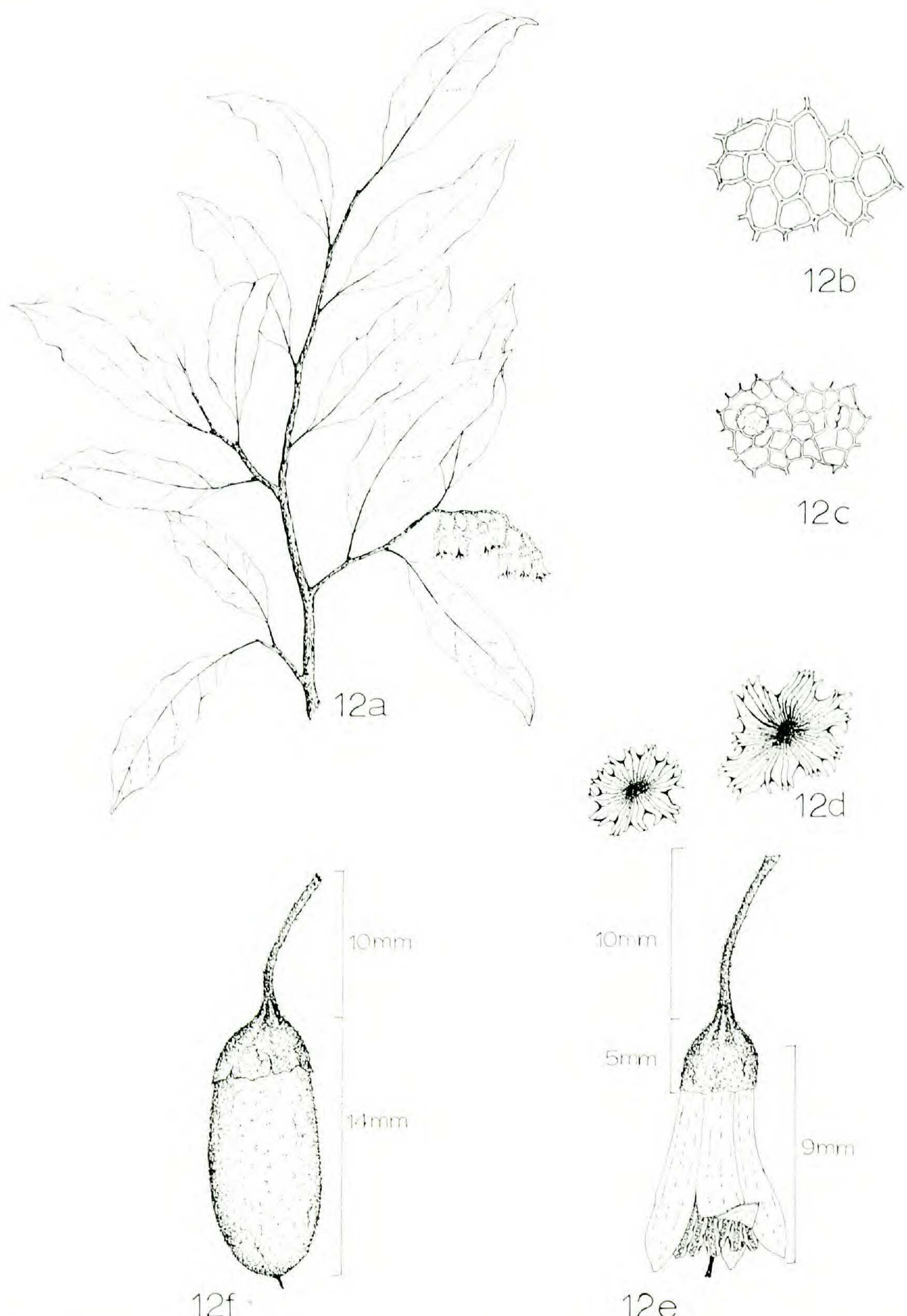


Fig. 12. *Styrax conterminus*: a. habit sketch; b, c. upper & lower leaf epidermis ($500\times$); d. trichomes on lower leaf surface ($128\times$); e. mature flower; f. mature fruit.

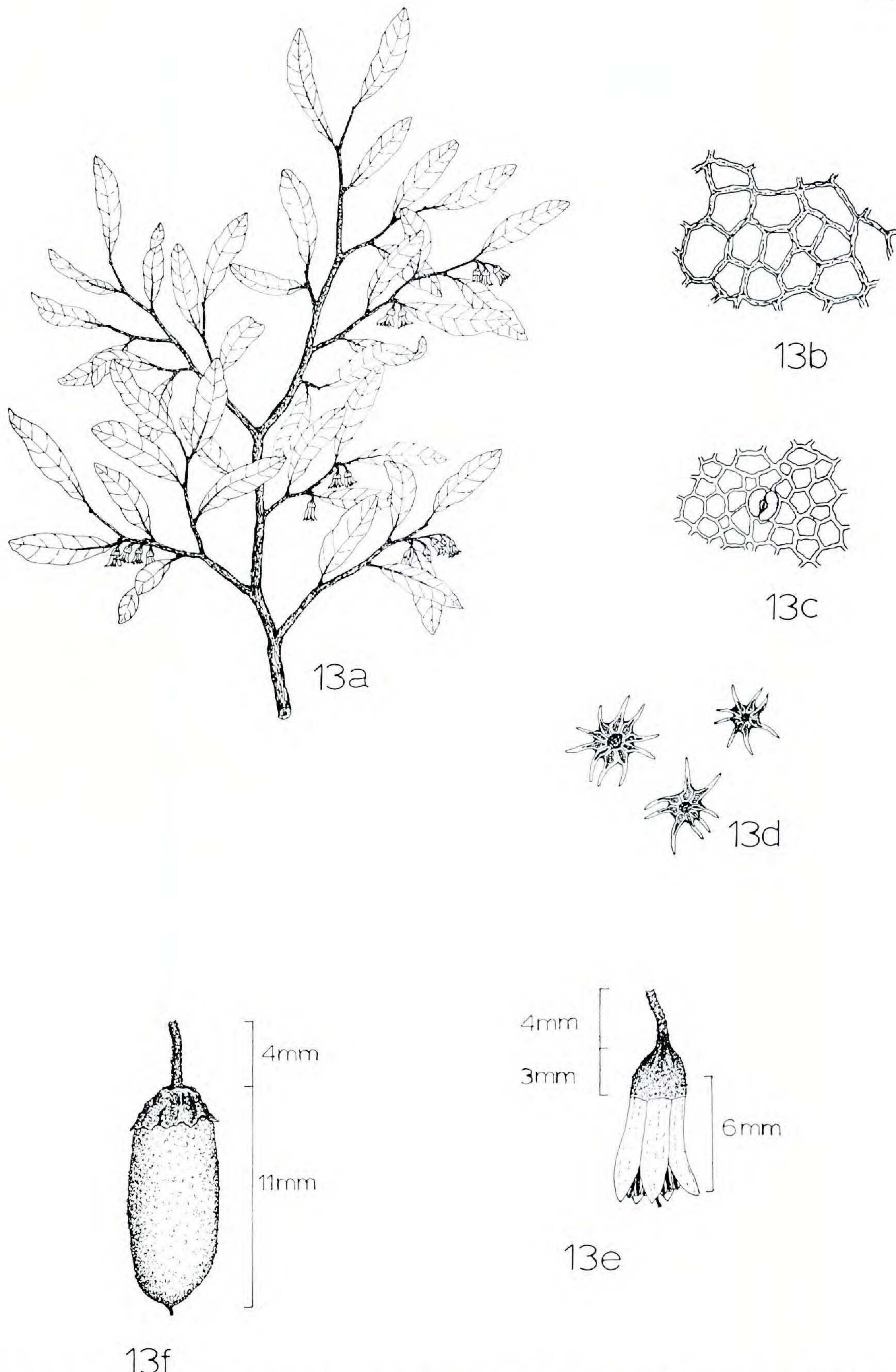


Fig. 13. *Styrax obtusifolia*: a. habit sketch; b, c. upper & lower leaf epidermis ($500\times$); d. trichomes on lower leaf surface ($128\times$); e. mature flower; f. mature fruit.

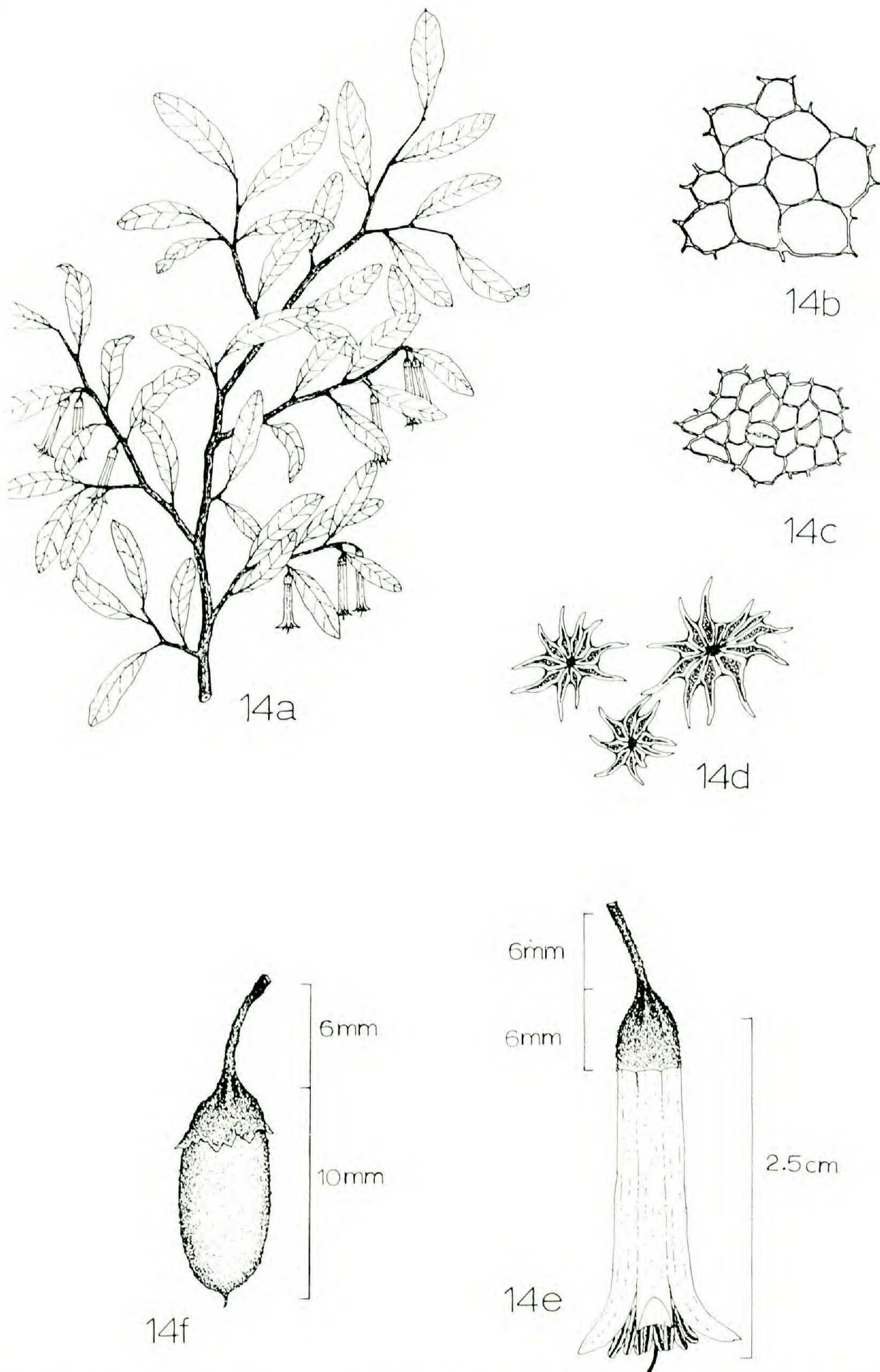


Fig. 14. *Styrax ochraceus*: a. habit sketch; b, c. upper & lower leaf epidermis ($500\times$); d. trichomes on lower leaf surface ($128\times$); e. mature flower; f. mature fruit.

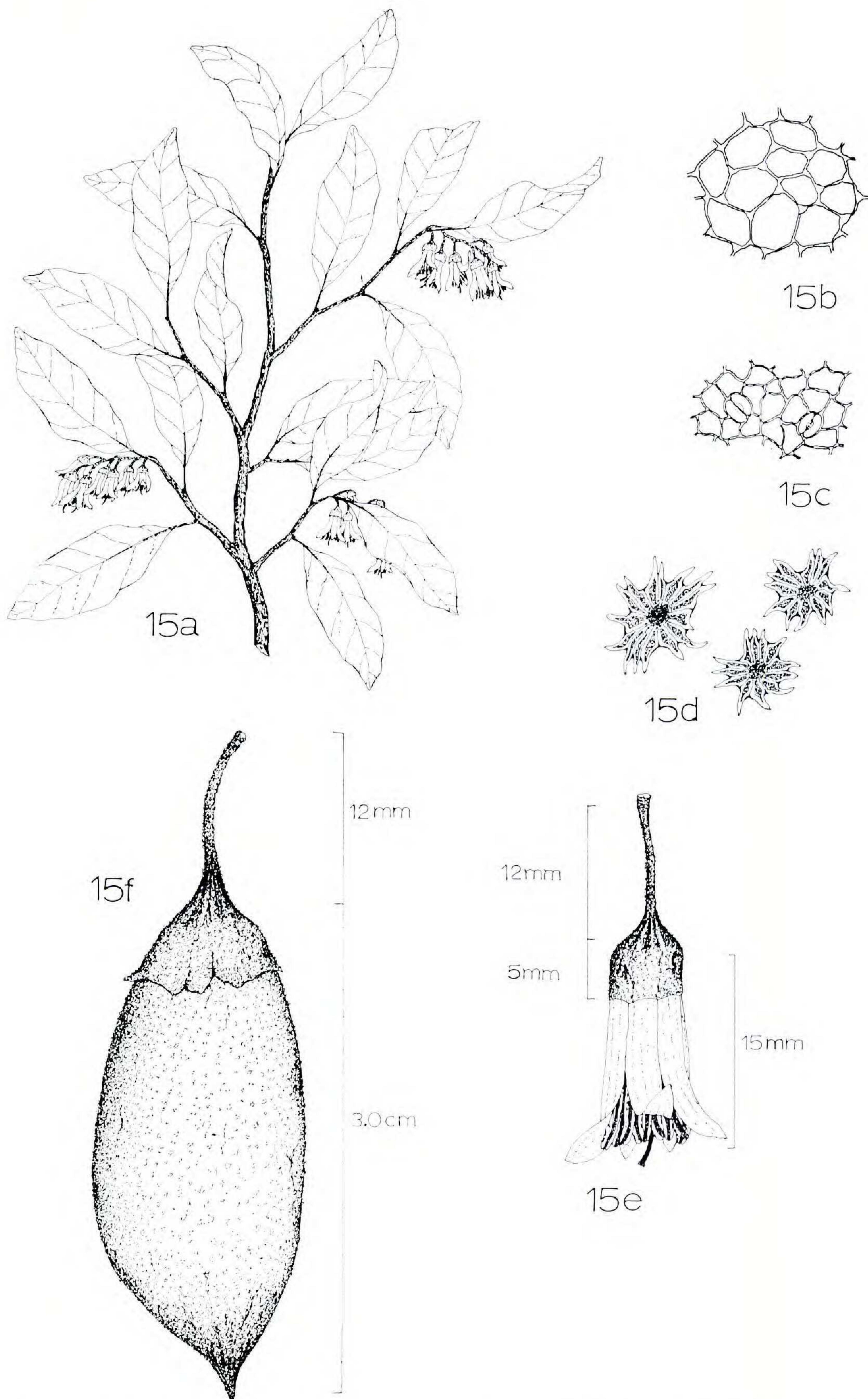
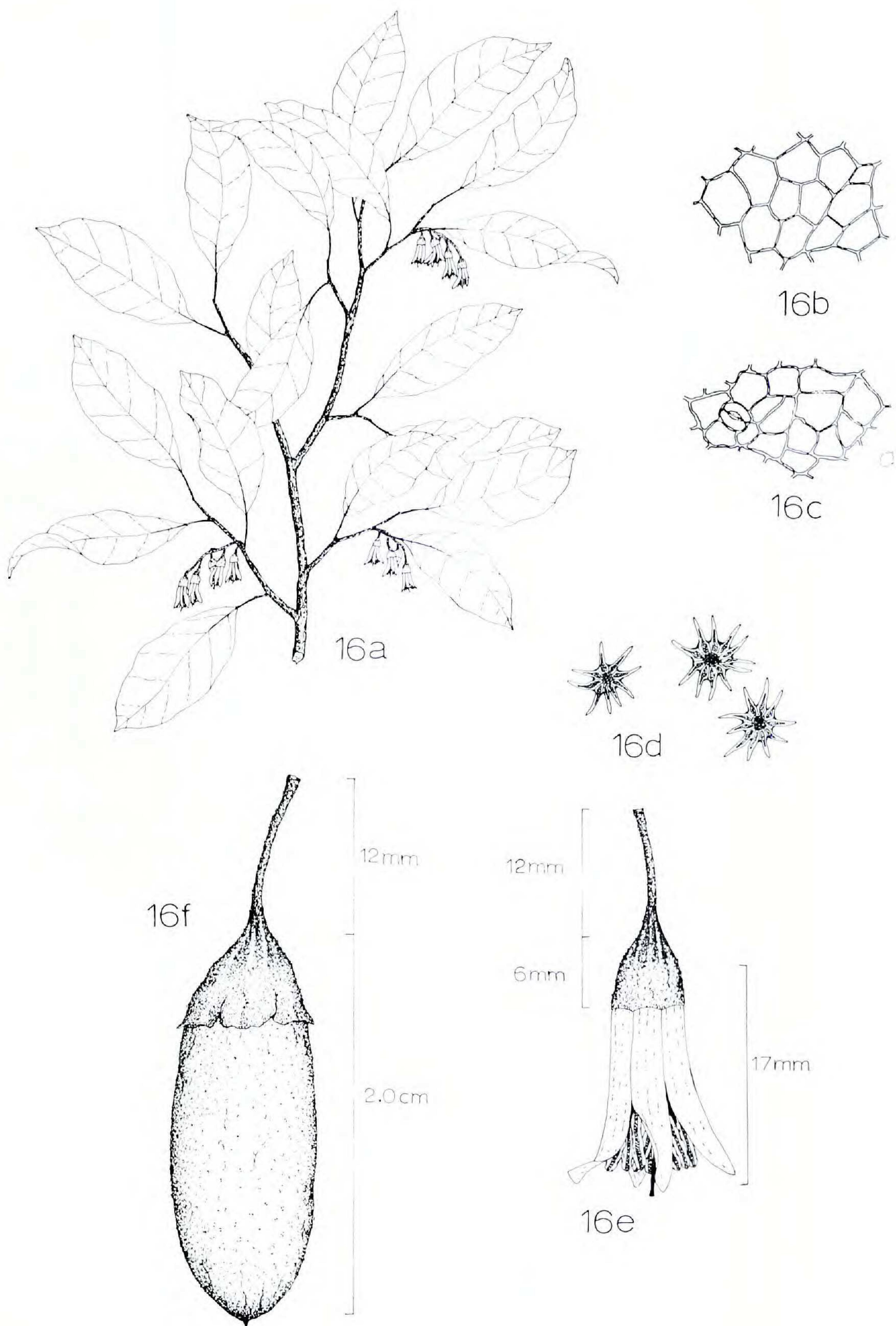


Fig. 15. *Styrax portoricensis*: a. habit sketch; b, c. upper & lower leaf epi-

dermis ($500\times$); d. trichomes on lower leaf surface ($128\times$); e. mature flower; f. mature fruit.

Fig. 16. *Styrax glaber*: a. habit sketch; b, c. upper & lower leaf epidermis ($500\times$); d. trichomes on lower leaf surface ($128\times$); e. mature flower; f. mature fruit.



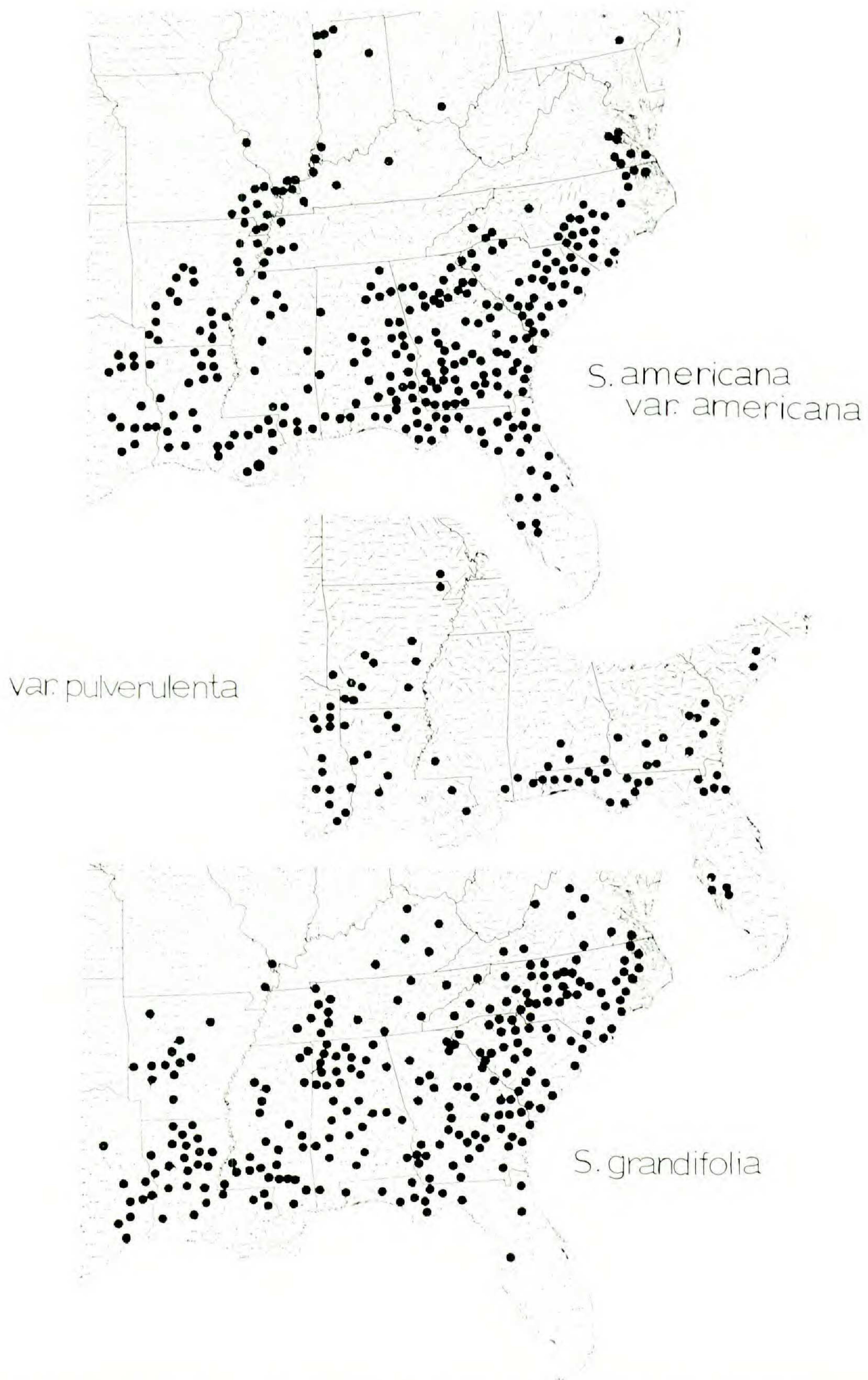


Fig. 17. Documented distribution of *Styrox americana* var. *americana*, *S. americana* var. *pulverulenta*, and *S. grandifolia*.

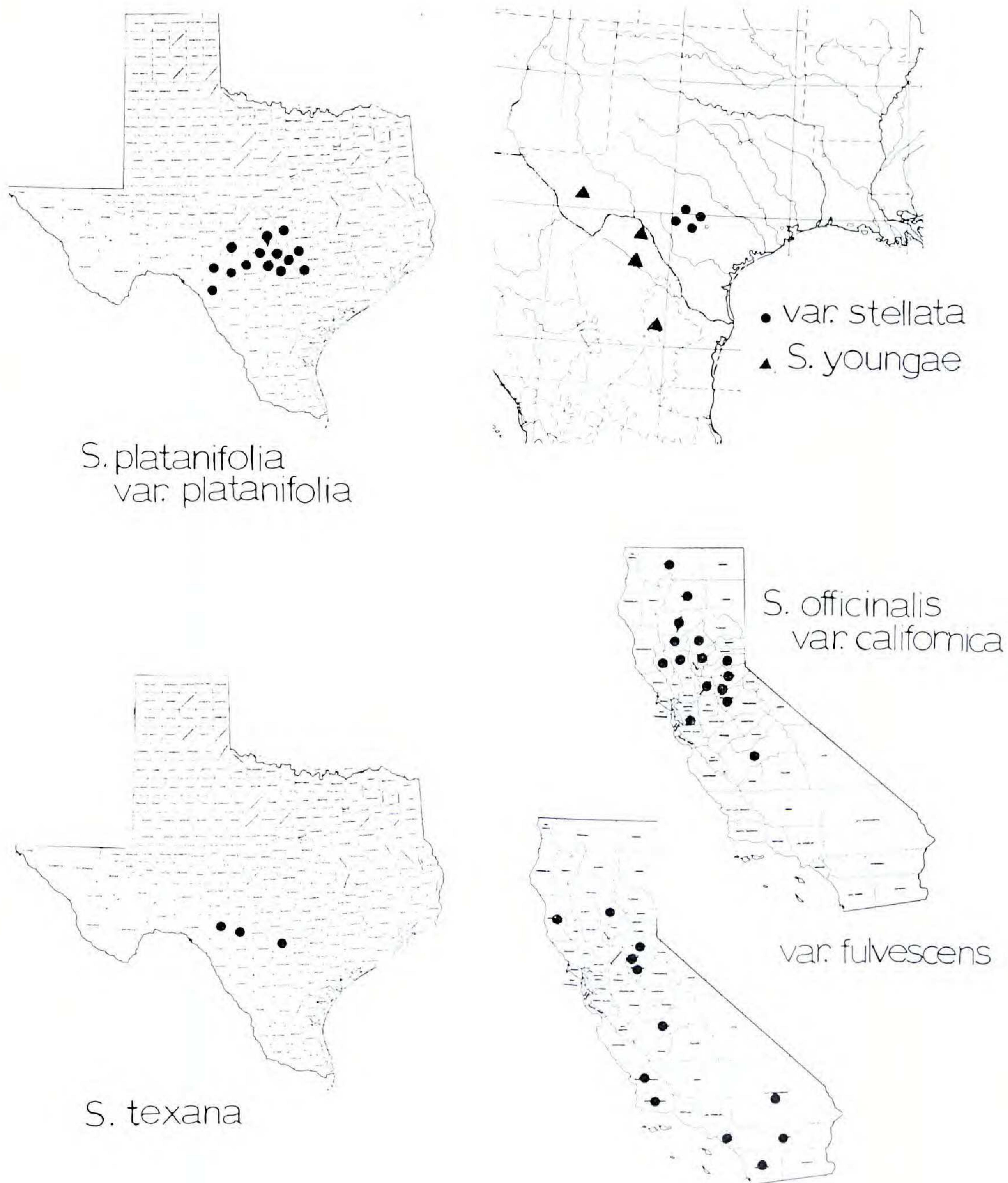


Fig. 18. Documented distribution of *Styrax platanifolia* var. *platanifolia*, *S. platanifolia* var. *stellata*, *S. youngae*, *S. texana*, *S. officinalis* var. *californica*, and *S. officinalis* var. *fulvescens*.

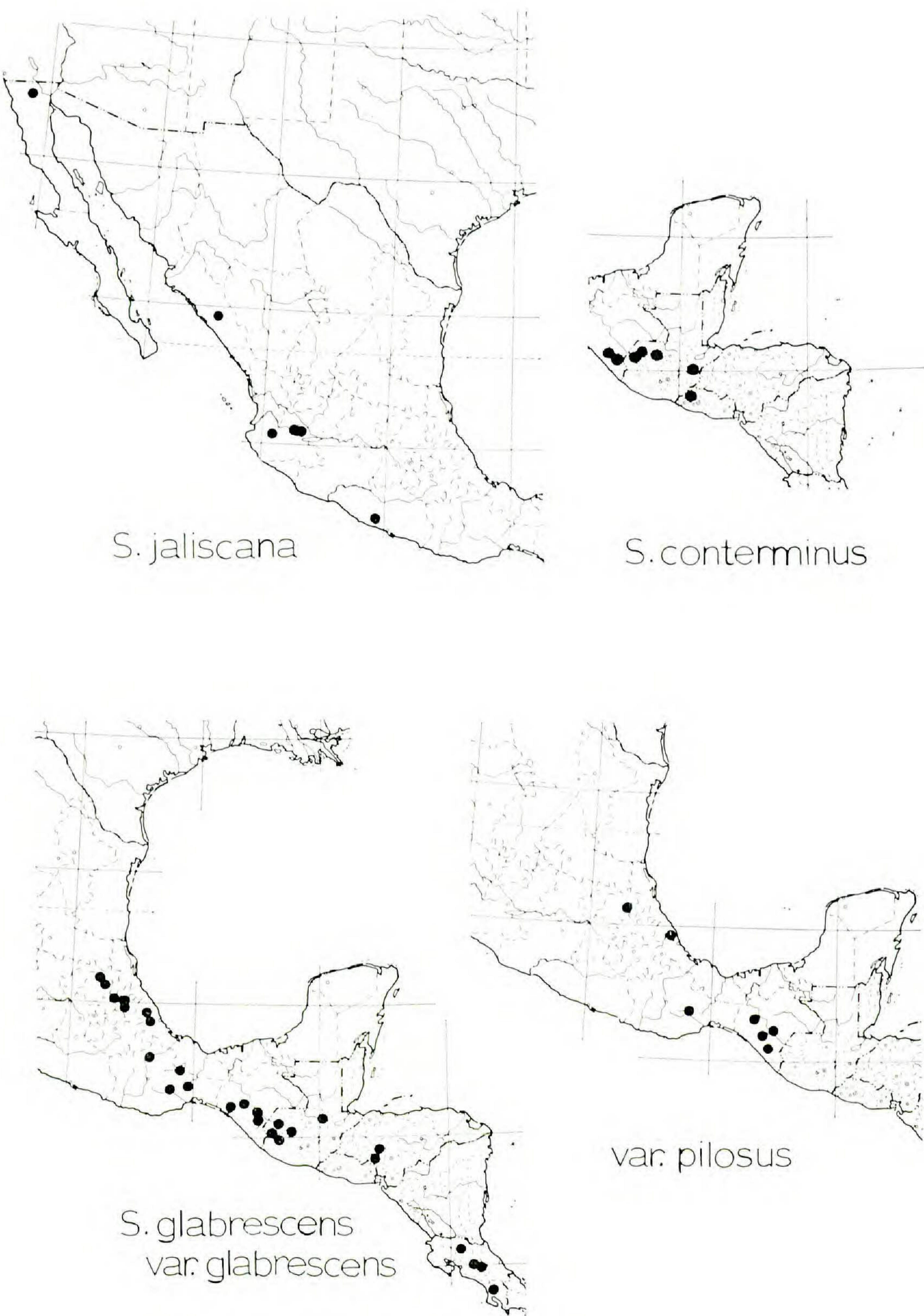


Fig. 19. Documented distribution of *Styrax jaliscana*, *S. conterminus*, *S. glabrescens* var. *glabrescens*, and *S. glabrescens* var. *pilosus*.



Fig. 20. Documented distribution of *Styrax argenteus* var. *argenteus*, *S. argenteus* var. *ramirezii*, and *S. argenteus* var. *hintonii*.

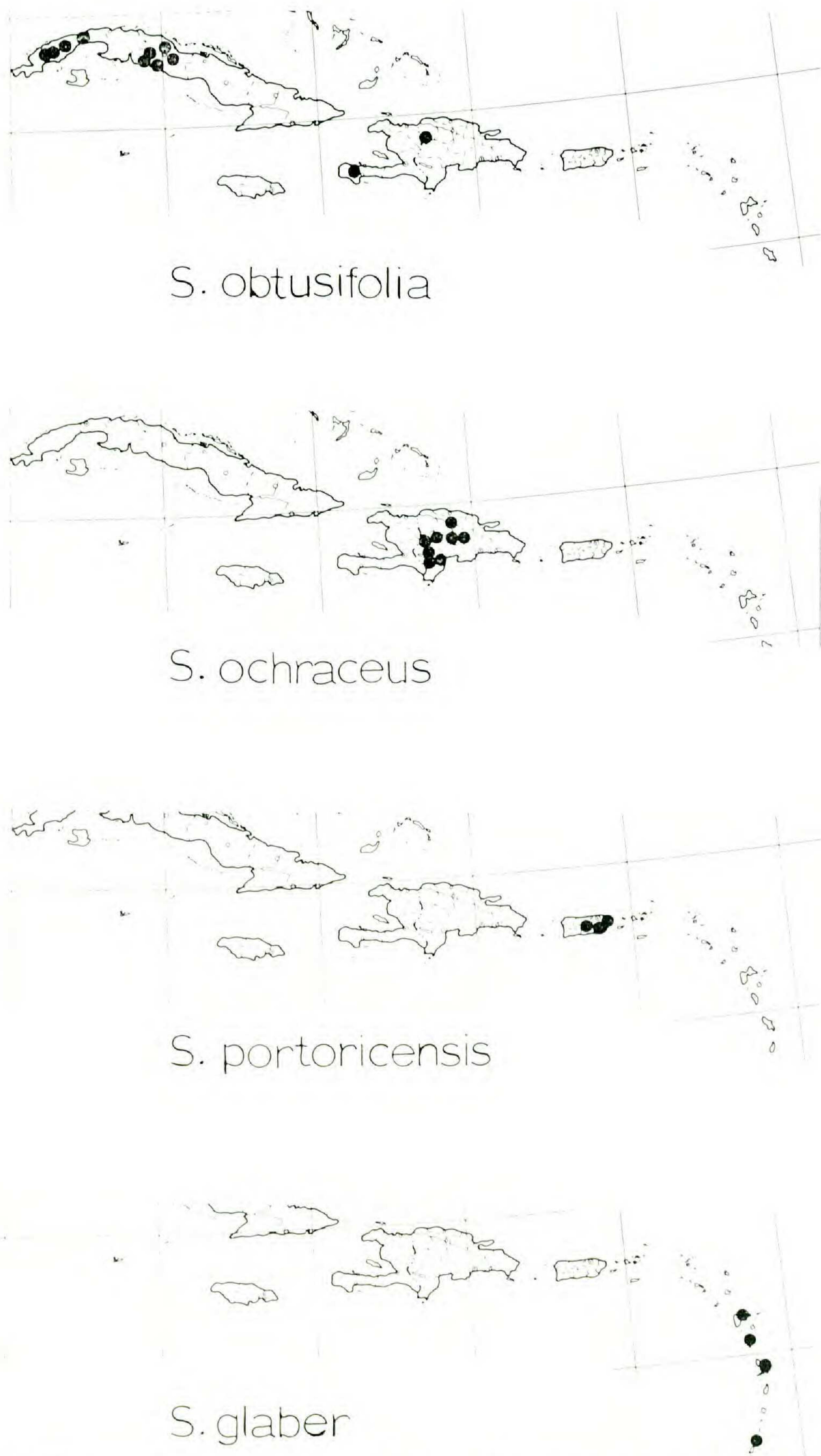


Fig. 21. Documented distribution of *Styrax obtusifolia*, *S. ochraceus*, *S. portoricensis*, and *S. glaber*.